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THE CITATION OF SOME GENERA OF THE LAURACEAE[1]

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IN THE COURSE of a review of the genera of Lauraceae occurring in the southeastern United States it has been necessary to verify the citations of the native and naturalized genera and their typification. Hardly any uniformity in these matters exists in the literature of this difficult family, especially in connection with groups published prior to C. G. Nees' basic monographic treatment in 1836. *Cinnamomum,* for example, is still being cited variously as of Linnaeus, Blume, Trew or Nees & Ebermaier. Still another author has been proposed for this genus and for *Persea* and *Sassafras* in recent papers by Kostermans (1952, 1957).

It is hoped that the notes which follow will help to clarify the bibliographic citation of these and other genera grouped by Linnaeus under his all-inclusive *Laurus* (Gen. Pl. ed. 5. 173. 1754). Supposing that the glands of the third series of stamens were a constant generic characteristic (rather than one of very nearly the entire family), Linnaeus lumped under his "452. LAURUS.* *Tournef.* 367." plants formerly treated as separate genera (and later restored to generic rank by one or more authors in spite of the Linnaean influence which lasted almost fifty years). Included by Linnaeus were "Cinnamomum *Herm.* H. L. B. 656. *Burm. zeyl.* 28: 1. Camphora *Gronov. Diss.* Persea *Plum.* 20. Borbonia *Plum.* 2. Benzoë *Boerh.* Sassafras *Off.*" In the Linnaean interpretation, each of these generic names was used for that of a species under *Laurus.*

Recently, in an historical review of the Lauraceae (1952) and in his synopsis of the family (1957), both works representing an enormous amount of time and effort and of great value toward an understanding of the group, Kostermans has accepted G. R. Boehmer's 1760 edition of C. G. Ludwig's *Definitiones Generum Plantarum* as the place of valid publication of *Cinnamomum, Camphora, Borbonia, Persea, Benzoin,* and *Sassafras.* While it is most certainly desirable to establish the earliest possible date for these names, in this instance the publication appears to be invalid

[1] Continuing a series of miscellaneous notes and papers on the flora of the southeastern United States made possible through the interest and support of George R. Cooley and a grant from the National Science Foundation.

under the International Code of Botanical Nomenclature. On page 63 of this edition, under "188. LAURUS. *Linn.* Ed. V. n. 452," following a generic description identical with that in the edition of 1747, come the pertinent lines: "*Sexus et numerus partium variat, staminum tubercula pro constanti generico charactere assumit Linnaeus; et ab eodem huc refertur.*" There follow the names and good short descriptions (here omitted) of:

LAURUS *Tourn.* 597.
CINNAMOMUM *Burm. Zeyl.* 28. CARVA *H. Mal. T. I. p.* 107.
CAMPHORA *Boerh. II.* 261.
BORBONIA *Plum. G.* 3.
PERSEA *Plum. G.* 44.
BENZOIN *Boerh. II.* 259.
SASSAFRAS *C. B. Pin.* 431.
LAURUS INDICA *Aldini licet monente Hallero Goett. p.* 15.

These are unnumbered, placed beneath *Laurus* in the fashion of similar notes and clearly intended synonyms throughout the book, and are in italics in the index (the usual practice for synonyms). The descriptions are also in italics, in contrast to the roman type of accepted genera in this work.

The earlier edition of Ludwig (1747) includes on p. 35 under "133. LAURUS. *Linn.*" the same generic description followed by the note "*Huc igitur a Linnaeo referuntur:*" and the same generic names of the later edition, with the exception of *Laurus indica* which was added by Boehmer along with more complete citations.

Clearly the names appended to *Laurus* were not accepted by either Ludwig or Boehmer, both of whom followed Linnaeus in construing that genus in its very broadest sense. They cannot be attributed properly to Boehmer for, being placed by him in the synonomy of *Laurus*, they must be regarded as invalid. (*Cf.* Art. 33, Internat. Code Bot. Nomencl. 1956.)

Although Boehmer's names are not acceptable, it would seem necessary to follow Rehder (1949) and Little (1953) in adopting those of Lauraceae from Trew in Blackwell's Herbal (1757, 1760). This work is a nomenclatural hodge-podge following no particular system, but *Sassafras*, *Cinnamomum*, and *Camphora* are adequately described and illustrated with clear and unmistakable references linking them to the corresponding Linnaean species. If the generic names now generally cited as dating from Miller, Gard. Dict. Abr. ed. 4. 1754, are legitimate under the Code, those of Trew must be equally acceptable. *Cinnamomum*, *Camphora*, and *Sassafras* of Trew antedate by a number of years the other possible authors of those names.

The citations which follow are not complete but include the earliest place of publication, the second earliest in most instances, and other data.

BENZOIN Fabr. Enum. Meth. Pl. Horti Medici Helmstad. ed. 2. 401. 1761, nom. rejic. (Type: *Laurus Benzoin* L. [= *Lindera Benzoin* (L.) Blume]). =

Lindera Thunb. Nova Gen. Pl. **2:** 44. 1783 (Type: *L. umbellata* Thunb.); Blume, Mus. Bot. Lugd.-Bat. **1:** 323. 1851, nom. cons. Non *Lindera* Adanson, Fam. Pl. **2:** 425. 1763.

BORBONIA Miller, Gard. Dict. Abr. ed. 4. 1754 (based on a mixture including at least *Persea* Miller and *Nectandra* Rol. ex Rottb.; *cf.* Kostermans, 1952); Adanson, Fam. Pl. **2:** 341. 1763 (a mixture, including *Persea, Nectandra, Ocotea* Aubl.). Non **Borbonia** L. 1753 (Leguminosae).

CAMPHORA Trew, Herb. Blackwell. Cent. 4, signature L. *t. 347.* 1760 (Type: *Laurus Camphora* L. [= *Cinnamomum Camphora* (L.) T. F. L. Nees & Ebermaier]); C. G. Nees in Wallich, Pl. As. Rar. **2:** 61, 72. 1831 (Type: *Camphora officinarum* C. G. Nees [= *Cinnamomum Camphora*]). = **Cinnamomum** Trew, sect. **Camphora** (Trew) Meissn. [attributed by Meissner to C. G. Nees].

Cinnamomum Trew, Herb. Blackwell. Cent. 4, signature M. *t. 354.* 1760 (Type: *Laurus Cinnamomum* L. [= *C. zeylanicum* Blume]); Blume, Bijdr. Fl. Nederl. Indië 568. 1826 (Type: *C. zeylanicum* [Garc.] Blume).

Persea Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.[2] (Type: *Laurus Persea* L. [= *P. americana* Miller, 1768]); Miller, Gard. Dict. ed. 8. 1768 (Type: *P. americana* Miller); Gaertn. f. Fruct. **3:** 222. *t. 221.* 1805 (Type: *P. gratissima* Gaertn. f. [= *P. americana* Miller]).

Sassafras Trew, Herb. Blackwell. Cent. 3, signature P. *t. 267.* 1757 (Type: *Laurus Sassafras* L. [= *S. albidum* (Nutt.) C. G. Nees]); T. F. L. Nees & Ebermaier, Handb. Med.-Pharm. Bot. **2:** 418. 1831 (Type: *S. officinale* T. F. L. Nees & Ebermaier, "*officinalis.*" [= *S. albidum*]).

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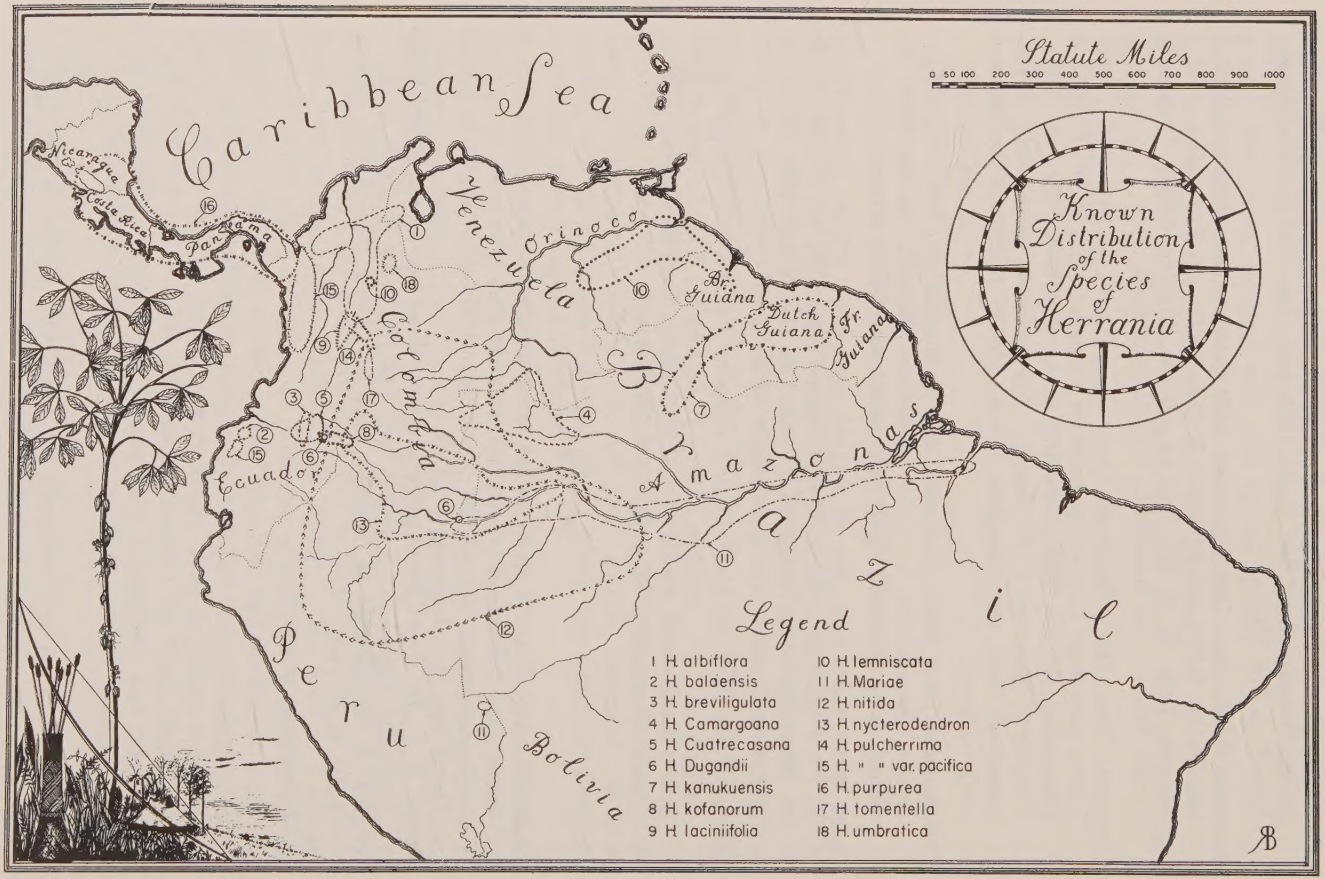
[2] Conservation unnecessary.


Statute Miles
0 50 100 200 300 400 500 600 700 800 900 1000
Known Distribution of the Species of Herrania
Caribbean Sea
Nicaragua
Costa Rica
Panama
Venezuela
Orinoco
Colombia
Br. Guiana
Dutch Guiana
Fr. Guiana
Ecuador
Amazonas
Brazil
Peru
Bolivia
Legend
1 H. albiflora
2 H. baldensis
3 H. breviligulata
4 H. Camargoana
5 H. Cuatrecasana
6 H. Dugandii
7 H. kanukuensis
8 H. kofanorum
9 H. laciniifolia
10 H. lemniscata
11 H. Mariae
12 H. nitida
13 H. nycterodendron
14 H. pulcherrima
15 H. " " var. pacifica
16 H. purpurea
17 H. tomentella
18 H. umbratica

A SYNOPSIS OF THE GENUS HERRANIA

RICHARD EVANS SCHULTES

With seventeen plates

> La flor se podrá mirar como la mayor maravilla del reino vegetal, y apenas se pudiera creer que la económica y sencillísima naturaleza hubiese gastado tantas cintas y atavíos para engalanarla casi con la ostentación de las modas.
>
> — *Eloy Valenzuela* (1784)

MORE THAN AN ACADEMIC INTEREST moves me to present this study of the sterculiaceous genus *Herrania*, a close relative of *Theobroma*, the genus of the cultivated cacaos. In recent years, the chocolate industry of the world has become increasingly alarmed over the ravages of certain fungal and virus diseases of the cultivated forms of *Theobroma*. These are so serious that the industry has waned almost to extinction in several parts of the world, and our sources of certain grades of chocolate are seriously threatened. Extensive investigations toward a control of the disease have been carried out in a number of scientific institutions; much has been done in plantations toward selection of resistant strains, and several attempts to do this from wild material have been made; furthermore, attention has been devoted toward the possibility of overcoming the difficulties through hybridization and other techniques.

It is my belief, however, that sooner or later an extensive program for selection of new germ plasm from the jungle must be initiated, if the chocolate industry is to be saved. Naturally, such a project would include all near allies of *Theobroma* (Schultes, R. E. "El género *Herrania*, pariente silvestre del cacao cultivado." Agric. Trop. 7: 43–48. 1951; "Le genre *Herrania*, parent sylvestre du cacaoyer cultivé." L'Agron. Trop. 6: 661–663. 1951). In 1952–53, the Imperial College of Tropical Agriculture in Trinidad and the Colombian Ministerio de Agricultura carried out jointly a very thorough study of *Theobroma* and *Herrania* in the Amazonian sector of Colombia. This study, which was headed by the late Prof. Richard E. D. Baker and Dr. Francis W. Cope, of the Imperial College, and which included half a dozen additional British and Colombian scientists, explored many of the major rivers of the region and made selections of interesting or outstanding material for the cacao-improvement scheme in Trinidad.

Herrania first attracted my attention in 1941, when I collected a then undescribed species in southern Colombia. The process of determining and describing this collection brought out the great need for a revisionary treatment of the genus. Nevertheless, in view of the sparse and fragmentary collections then in our herbaria, as well as the unavailability during the war of material from European institutions, it seemed advisable to await a more favorable time before undertaking such a revision.

From 1941 to 1953, I was engaged in almost uninterrupted field studies (chiefly of the genus *Hevea*) in the Amazon Valley. In connection with this work, it was often possible for me to give special attention to *Herrania* in its native habitat and to make collections over a wide area. This intimate association with the living plants enabled me to study a number of morphological and ecological characters which are lost in the preparation of herbarium material. It has also been possible, in some cases, to study and collect fruits which, although often wanting in our herbaria, can be highly significant from the taxonomic point of view.

In addition to field studies, I have consulted all available specimens from the principal herbaria in the United States and South America in the preparation of the following synopsis. Furthermore, in 1947 and again in 1950, I was able to study the collections preserved in England and on the continent of Europe.

Although it would seem that sufficient material upon which to base an admittedly preliminary treatment of *Herrania* has now been consulted, we must realize that certain concepts are still rather poorly understood. Further field studies will almost certainly lead to alterations in our present treatment and will undoubtedly enhance our knowledge of the composition and geographic distribution of the genus.

ACKNOWLEDGEMENTS

So many friends have aided me in so many ways in both the herbarium and the field that I find it difficult to thank them all individually. The late Professor Oakes Ames, of Harvard University, followed my field and herbarium investigations of *Herrania* from their beginning and, by letter and conference, stimulated me with his many suggestions and with his deep interest in economic botany. It is with warm appreciation that I thank Professor Paul C. Mangelsdorf, director of the Botanical Museum of Harvard University, for his constant encouragement in the work of preparing this study of *Herrania*. My colleagues at the Botanical Museum, especially Dr. Albert F. Hill and Mr. Charles Schweinfurth, have likewise given generously of their time, advice and encouragement throughout the years of preparation of this study. My deep gratitude must go to Dr. E. W. Brandes and Dr. Robert D. Rands, who directed my work on *Hevea* rubber for the United States Department of Agriculture, for their encouragement and understanding of my botanical activities which, like the *Herrania* investigation, were not directly concerned with my regular studies in latex-bearing plants. Dr. N. Y. Sandwith of the Royal Botanic Gardens, Kew, has been most generous with his help during the last few years of this study. To Dr. Armando Dugand, former director of the Instituto de Ciéncias Naturales in Bogotá, and Dr. Felisberto Camargo, former director of the Instituto Agronômico do Norte in Belém do Pará, Brazil, I am especially indebted for their interest and for many kindnesses during my years of field work. Mr. Gordon W. Dillon, the late Señorita Inés de Zulueta and Miss Helen Schieffer deserve my warmest thanks for their drawings which were published in some of my earlier taxonomic papers on *Herrania*.

It is difficult for me to express adequately my gratitude to Mr. Elmer W. Smith for the highly accurate and artistic drawings which illustrate this synopsis. Sincere thanks go also to the American Cocoa Research Institute and the National Science Foundation for generous grants of money towards the illustrating of my taxonomic studies in this genus of close relatives of the chocolate plant.

My deepest appreciation is due to the numerous members of the Anglo-Colombian Cacao Collecting Expedition, especially to the late Prof. Richard E. D. Baker and to Dr. Francis W. Cope, together with which Expedition I was able to spend many months in the field and to test the workability and completeness of this synopsis of *Herrania*.

To the directors and staffs of the following American botanical institutions I send my thanks for the loan of specimens or for their kind permission to consult material in their care; the Gray Herbarium, the Arnold Arboretum, and the Economic Herbarium of Oakes Ames (Harvard University); the Bailey Hortorium (Cornell University); the New York Botanical Garden; the Missouri Botanical Garden (St. Louis, Mo.); the Chicago Natural History Museum; the United States National Herbarium (Washington, D. C.); the United States National Arboretum [Herbarium] (Beltsville, Md.); the Philadelphia Academy of Natural Sciences; and the Yale School of Forestry (New Haven, Conn.). I am deeply grateful also to the officers of the following European and South American botanical centers for their many courtesies during my periods of study in their herbaria; the Royal Botanic Gardens (Kew) and the British Museum (Natural History) (London); the Botanisch Museum en Herbarium (Utrecht); the Rijksherbarium (Leiden); the Universitats Botaniska Museum (Copenhagen); the Museum National d'Histoire Naturelle (Paris); the Jardín Botánico (Madrid); the Conservatoire Botanique (Geneva); the Herbier Boissier (Geneva); Jardin de l'État (Brussels); the Botanische Staatssammlung (Munich); the Naturhistoriska Riksmuseum (Stockholm); the Instituto de Ciéncias Naturales (Bogotá); the Facultad Nacional de Agronomía (Medellín); the Instituto Agronômico do Norte (Belém); the Museu Goeldi (Belém); the Jardim Botânico (Rio de Janeiro); the Instituto Miguel Lillo (Tucumán); and the Instituto Interamericano de Ciéncias Agrícolas (Turrialba, Costa Rica).

HISTORICAL NOTES

Herrania was described by Justin Goudot in 1844 and was named in honor of General Pedro Alcántara Herrán (1800–1872), president of New Granada (Colombia) from 1841 to 1845. In spite of civil unrest in the country, Herrán showed much interest in the botanical investigations of Colombia during this period. It is therefore quite appropriate that this genus, which has its center of diversification in Colombia, should bear his name.[1]

[1] It is equally appropriate for me to express, in this paper, summarizing our present knowledge of *Herrania*, my gratitude to Dr. Alvaro Herrán Medina, his great grand-

The specimens upon which this genus and its first two species, *Herrania albiflora* and *H. pulcherrima*, were based had been brought to the attention of the scientific world long before the actual publication of the genus in 1844. At the meeting of the Linnean Society of London on January 15, 1828, Goudot referred to "a plant of the genus nearly akin to *Theobroma* from which it differs chiefly in habit, in the form of the calyx, and the structure of the stamens . . . 'Arbuscula foliis digitatis, quinatis' " (Philosoph. Mag. 3: 132. 1828). Before presenting his diagnosis of *Herrania*, Goudot devoted much careful study to the new genus, for he wrote "[since 1828] . . . I have had frequent occasions to study these plants and to assure myself that they ought to constitute a distinct genus" (Ann. Sci. Nat. Paris III. 2: 229. 1844). Goudot's original diagnosis of *Herrania*, reproduced below, is so detailed and so carefully prepared, with such a clearly outlined concept as to relationship, that now there is no need to alter either the description or the concept, and this in spite of the fact that the number of species known has been measurably increased.

Long before *Herrania* was actually described, however, several species were recognized as distinct from *Theobroma*. The Botanical Expedition of Mutis in New Granada (Exped. Bot. Mutisii Novae-Granat.), which was carried out in Colombia by a capable and devoted group of scientists under the leadership of Padre José Celestino Mutis from 1783 to 1808, collected some 4055 specimens, including several species of *Herrania*. The greatest heritage of the expedition is the collection of water-color paintings of Colombian plants, numbering 6900 plates and representing 2800 species. The plates, in perfect condition, are preserved in the Jardín Botánico in Madrid and their publication has only recently been initiated. I was fortunate in 1950 to have an opportunity to study many of these plates, but permission to publish any of them could not be granted.

Amongst the 6900 plates, there are several extraordinarily artistic and accurate illustrations representing three species of *Herrania*. These plates, labelled simply "*Theobroma*" by the artists, are all included in Volume No. 28 under number 5333. They were first determined as representing several concepts of *Herrania* by Triana, who annotated each plate in pencil and signed his annotations. These plates were made about half a century before the genus *Herrania* and the three species so beautifully represented by the Mutis plates were described by Goudot.

Recently, a most significant discovery related to the work of the Mutis Expedition was made. The Colombian historian, Dr. Guillermo Hernández de Alba uncovered, in 1950, a beautifully preserved manuscript prepared by Padre Eloy Valenzuela, one of the most active members of the Expedition. The manuscript is without title, but Dr. Enrique Pérez-Arbeláez entitled it "Diario de la Expedición Botánica del Nuevo Reino de Granada

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nephew, and my good friend. Dr. Herrán Medina, who served for a number of years as Colombian Consul General in Manáos, Brazil, followed the progress of my work in the Amazonian area of both Colombia and Brazil with enthusiastic interest and performed innumerable services and favors without which that work would have been much more difficult.

dirigida por Don José Celestino Mutis y llevado por Eloy Valenzuela desde el día 29 de abril de 1783 al día 8 de mayo de 1784" (Pérez-Arbeláez, E., Un hallazgo histórico y científico: el diario de D. Eloy Valenzuela. El Tiempo (Bogotá), February 11, 1951). Thanks to Dr. Pérez-Arbeláez, I may quote in full this extraordinarily detailed description of a species of *Herrania* which Valenzuela wrote in his diary and publish a photograph of one of the pages in Valenzuela's own hand.

This description, referring without doubt to *Herrania pulcherrima*, is the earliest reference to *Herrania* of which we have any knowledge. In it, Valenzuela clearly sets forth his recognition of the plant as different from the *cacao común* (*Theobroma Cacao*). Goudot's validly published diagnosis and description of *Herrania* is, for all practical taxonomic purposes, the earliest; but, for historical reasons, I am publishing herewith a transcript of Valenzuela's diary-notes on his *cacao esquinado*. There is every reason to believe that the plant to which these notes refer grew in the vicinity of Mariquita, where the Expedition carried out a great part of its labor.

Día 13 de marzo de 1784. Sin concluir el Guácimo real, se trabaja hoy en el cogollo de la theobroma de cintillas o Cacao esquinado. El otro día repetí mi visita a la mata y el dueño me dijo que los cuatro tallos que tiene aproximados corresponden a una raíz sola. Los tallos serán hacia el pie tan gruesos como el dedo pulgar sin ramo alguno tupidísimos juntamente con las hojas de pelo chico, apelmazado y amonado; por dentro blanco, fibroso, ligeros; la parte leñosa es radiada con líneas que tiran para el centro; el meollo gruesesito, blanquísimo, esponjoso, regado de puntos lucientes y cercado con algunas fibras huecas. Una de estas partes despide algo de un licor diáfano y viscido. Hojas son alternas bastante inmediatas, patentes, decusadas. — Estípulas dos laterifolias algo retiradas opuestas adpressas, subuladas pollicares y de la misma pubescencia que el tallo y hojas. — Flor: agregadas axilares y supraaxilares, peculiares de la parte inferior; pedícelos sencillos, recurvos o levantados para arriba.

Día 14. Domingo.

Día 15. Se trabaja en dibujar el tallo del cacao esquinado o theobroma de cintillas en la parte que carga las flores y como vinieron muchas de éstas, he tenido lugar de hacer el apunte casi por entero.

Cacao Esquinado. Raíz. Tallo: De la altura humana, derecho, rollizo, sencillísimo, tupidísimo de pelo chico, grueso al tanto del dedo pulgar: y parece que acompañado de 3 a 4 sobre una raíz; su color parduzco sucio, hacia el pie es algo desnudo y color de café y aquí mismo tiene la epidermis menudamente hendido-reticulada y algo levantada. — La corteza es gruesesita, verdosa debajo de la epidermis y flexibilísima, el interior blanco, fibroso, ligero y en el corte transversal se ve radiado con rayas que tiran al meollo desde la misma corteza: este es blanquísimo bofo y cercado de orifícios capilares por donde mana un jugo muy cristalino y gelatinoso.

Hojas: Grandes, alternas, túpidas, de pelo chico, 1-partidas hasta el mismo pezón común. — Pezón: común: patentes, pedales, multisulcados a lo largo y geniculados en los extremos. — Hojuelas: cuneiformes en la mitad inferior, escabradas por encima, membranáceas, y de bordes enteros, regados de puntas rigidiúsculas; la mayor excede al pezón común: las anteriores chicas obovato-

oblongas, obtusas con punta: las exteriores se ensanchan desde la mitad y abren en lacinias pinnadas, anchas, acuminadas, de las que son más grandes las dos primeras, más anchas las 3 terminales. En algunas hojas se suele añadir una chica y roma antes de las primeras. — Venas: paralelas, rectas, distantes. — Estípulas: 2 laterifolias, algo distantes de la axila, subuladas adpressas, pollicares y conformes a la extensión del tallo.

Flor: amontonadas, túpidas, axilares y supraaxilares en la parte inferior del tallo y casi siempre en las axilas desnudas, pollicares ligeramente olorosas y de color purpúreo, o bien de carmín profundo. — Pedúnculos: ningúnos. — Pedícelos: sencillos, levantados, delgadisimos por el pie y con dos o tres subulas cortas. — Cáliz: periantio monófilo, coriáceo, colorido, paludo exteriormente; antes de abrir es cerrado, ovado, obtuso; no se divide hasta cerca de la base en 3 partes cóncavas, enteramente reflexas, semipollicares; la una aguda; las dos anchas y agudamente semibífidas; parece que por su naturaleza es semiquinquéfido agudo y que al reflectar se hiende algo más, y no se apartan algunas veces los tres segmentos.

Nectarios: de 5 piezas, subrotundas, chicas, convexas exteriormente, embroscadas hacia adentro, plegadas y venulosas longitudinalmente y puestas alrededor del receptáculo: sus apéndices: son otras tantas cintillas angostas lineares, con 6 pollicares corridas a lo largo de dos o más venitas de color más subido. Antes de abrir están envueltas en piezas paradas sobre los pétalos y el color tira al amarillo.

Corola: de 5 piezas alternas con las del nectario y más interiores, lanceoladas, derechas, patentes de una longitud con el periantio, surcadas por encima a lo largo y cuadunadas ligeramente en la base.

Estambres: de 10 filamentos nacidos del lado de los pétalos, cortados, gruesos, recurvados para afuera, apareados y aproximados por los apices; anteras lineares, univalves, rayadas a lo largo, convexas, adnatas, a otras tantas lacinúlas de los filamentos, blancas y escondidas en el seno de los nectarios; 4 están en un filamento y 2 en el lateral. Estas forman como un ángulo y las primeras forman dos, metido el uno en el otro.

Gérmen: superior, pentágono, pyramidal, hirsuto, chico, de color herbáceo. — Estilo único linear, subduplo de la altura de los pétalos. — Estigma un poco obtuso y parece sencillo.

Fruto: bayas sentadas sobre la flor marchita, o bien mazorca ovada acuminada, tripolicar, 5 angular verde lustrosa y regada de tomento caedizo; el acumen es entero algo oblícuo; los ángulos levantadísimos, anchos, enteros, sólidos, venulosos lateralmente y alternan con 5 venas gruesas, algo anguladas, extendidas longitudinalmente por la depresión de ellos; la corteza blanda quebradiza, subglutinosa en la partidura, blanca y destituída de ángulos por dentro. Meollo ovado, 5 surcado, libre de la corteza y prendido por la base. — Granos: 70 convexo-angulados, rugoso-reticulados, coloridos de rosado blanquísimo, arilados con un saco fibroso empapado en jugo agridulce, y aproximados como en 5 hileras con alguna pulpa intermedia. — Receptáculo común, leñoso y central; parciales filiformes.

El interior . . .

El córculus asoma la cabecilla en la superficie interior . . . Cotiledones sin las complicaciones del cacao común.

Hojas seminales:

Tengo puestos algunos granos de tierra húmeda para ver si nacen y con esto determinar el modo con que se explica su interior y el tiempo que se necesita.

Nace con mucha frecuencia en el monte y rozas de esta inmediación: el grano amargo y sumamente mantecoso, dicen ser apetecido y consumido por los micos.

La flor se podrá mirar como la mayor maravilla del reino vegetal y apenas se pudiera creer que la económica y sencillísima naturaleza hubiese gastado tantas cintas y atavíos para engalanarla casi con la ostentación de las modas.

El periantio por fuera es de color acanelado, sucio salpicado de carmín, casi borrado. Por dentro es lustroso y de carmín hermoso.

Nectario: en el fondo es blanquecino o descolorido; las venitas y pliegues son de púrpura oscura. Las cintillas son carmesíes con venas oscuras.

Pétalos de púrpura afinadísima sub-oscura.

Estambres: en los filamentos son carmesíes y en las ánteras blancos.

Gérmen: pálido verdoso. Estilo purpúrea; estigma blanco.

Mazorca verde: por dentro sub-rósea.

Día 16. Se trabaja hoy en la hoja del cacao esquinado.

ECOLOGICAL PREFERENCES OF SPECIES OF HERRANIA

Herrania is distributed from sea level to about four thousand feet, but the altitudinal range of each species is often strictly limited. *Herrania purpurea* has been collected at sea level, and most of the specimens of this species are from localities below two hundred feet. *Herrania Mariae* occurs on the great flat Amazon planada from sea level at the mouth of the Amazon River to approximately three hundred and fifty feet in the western parts of the Amazon Valley. *Herrania nitida* and *H. tomentella* can be found in the western Amazon and Orinoco drainage-areas, from about two hundred and fifty feet above sea level up to the base of the Andes at about nineteen hundred feet. *Herrania albiflora* inhabits the slopes of the Andes between about three hundred and three thousand feet, thus exhibiting a more surprising altitudinal tolerance. The only known collection of *H. umbratica* was taken at about twenty-one hundred feet. Although the type collection of *H. pulcherrima* was made on the eastern slope of the Colombian Andes at about fifteen hundred feet altitude, most of the other collections are from the central Andean regions at about three thousand feet, with a distinct variety near sea level in western Colombia. Apparently rather intolerant of altitudinal variation is *Herrania laciniifolia*, which is known only from regions between three and four thousand feet. One of the species which seems to be confined to a narrow altitudinal range is *H. breviligulata* known from two collections from the eastern slopes of the Andes between eighteen and twenty-five hundred feet. The occurrence of *H. Camargoana* merits special mention, for it is unknown except in the upper Rio Negro basin of Brazil and Colombia, where it is found near or on the summits of barren granitic mountains rising to an altitude of about five hundred feet above the level of the river (or approximately twelve to seventeen hundred feet above sea level) and, rarely, in sandy riverside savannahs. *Herrania Cuatrecasana*, *H. Dugandii*, *H. kofanorum* and *H. nycterodendron* appear to be confined to the dense forests of the western-most parts of the Amazon Valley at an altitude of from three hundred to one thousand feet. *Herrania lemniscata* is found between four hundred

and three thousand feet and *H. kanukuensis* between four hundred and one thousand two hundred feet.

The species of *Herrania* do not seem to be exacting in their soil requirements, with the single exception of *H. Camargoana* which prefers and, actually, is found exclusively on sterile white sand and on the most inhospitable of rocky slopes strewn with granite blocks and often nearly devoid of soil. Most species thrive on well-drained slopes, but I have seen *Herrania purpurea* in the northwestern part of Colombia along the banks of rivers where, in the rainy season, the plants stand in from four to six feet of water. Similarly, *Herrania Mariae* often grows in Amazon forest which is subject to deep flooding half the year. *Herrania lemniscata* is also reported to grow in "mixed forest in swamp and on rather swampy soil" or "en selva anegada en la estacion lluviosa." The widely distributed *Herrania nitida*, in the Amazon Valley, is found usually just above the reach of the deep annual inundation, although occasionally it occurs where a few feet of water may stand for several weeks; it cannot, however, be classified as a flood-tolerant species.

There is one point which stands out in relief concerning the ecology of the various species of *Herrania*: both in altitudinal tolerance and in topographical preference there is a tremendously wide range within the genus. Some species seem to be extremely exacting, whereas others show an unbelievable tolerance in both altitudinal and topographical distribution.

Although all species of *Herrania* are primarily forest trees, a number act like weeds and propagate rapidly in agricultural clearings. The heliophilic tendency is especially marked in *Herrania nitida*. In the Amazon area, especially in Indian settlements, trees of *Herrania* are never sacrificed in the clearing of a field for planting or in the weeding of a cultivated patch. Since most cultivation is attempted on land above the reach of the annual flood, the species most commonly met with under conditions of partial human care is *Herrania nitida*. The only reason for not cutting down *Herrania* trees is, apparently, the esteem in which the natives hold the acidulous pulp surrounding the seed. Under conditions of ample room and sunlight, many more fruits mature than in the forest, and man is thereby repaid for his little consideration in sparing the tree. This toleration of the tree in planted fields is undoubtedly the basis of occasional reports that *Herrania* is sometimes cultivated. I have never seen *Herrania* under conditions of cultivation, nor have I been able to find reliable reports in the literature or on herbarium specimens to this effect.

USES OF SPECIES OF HERRANIA

As has been pointed out above, the principal importance of *Herrania* lies in its potentialities as a source of new germ-plasm in a possible hybridization program with the cultivated species of *Theobroma*.

In addition to this potential use, a few species find employment among native peoples Everywhere *Herrania* trees are left standing in cultivated ground, because the white, acidulous pulp in which the seeds are embedded

is eaten. Apparently this pulp is most delicious just before complete ripening of the fruit, and for this reason, it is often difficult to find a mature capsule. It is said that monkeys also search for the fruit as a food. Among the Ingano Indians of Mocoa, in the Putumayo of Colombia, the ashes of the bark of *Herrania breviligulata* are employed to dry up and "cure" infected wounds and ulcers (*Schultes & Smith 2050*). In British Guiana, according to notes accompanying *Archer 2514, Herrania lemniscata* is utilized in the preparation of a "beverage like chocolate." Similarly, Pittier reports (Plantas Usuales de Costa Rica. 72. 1908) that the Bribrí Indians of Costa Rica employ the seeds of *Herrania purpurea* to make a bitter drink. It has been reported (Van Hall, Cacao. ed. 2. 74. 1932) that formerly, in northern Colombia, the seeds of *Herrania albiflora* were purposely mixed with those of commercial cacao to improve the flavor of the chocolate and that these same seeds were often used to prepare a bitter febrifuge. *Herrania Mariae* seeds were formerly found as an adulterant in "Pará cacao" (Van Hall, loc. cit.).

RELATIONSHIPS AND TAXONOMY

Herrania appears taxonomically to be intermediate between *Guazuma* and *Theobroma*. It approaches *Guazuma* in the placement of its anthers but has an entirely different habit and fruit. It can be separated from *Theobroma* immediately by its habit (having compound-digitate leaves and, in general, comprising small, delicate and slender treelets). It further differs from *Theobroma* in the placement of its stamens, in the number of divisions of the calyx, in the length and form of its ligules, in its wood anatomy and in the structure of the pollen grains. The fruit of *Herrania* resembles, in outward form, that of *Theobroma*, but the seeds of *Herrania* have thick cotyledons which are almost entire and which are apparently not folded. The field botanist has perhaps a better opportunity of noting the differences between *Theobroma* and *Herrania*, for, in addition to the technical characters listed above, he is able to appreciate the great difference in habit and to observe that the jorquetting habit of branching, so characteristic of *Theobroma*, is not found in *Herrania*.

Although it would appear, on the basis of a taxonomic and morphologic examination of recent collections and field studies, as well as on experimental evidence, that *Herrania* may very justifiably be considered as a genus distinct from *Theobroma*, it has, in the past, usually been relegated to the position of section or subgenus under *Theobroma*. Schumann (in Martius, Fl. Brasil. 12(3) : 70–72. 1886), for example, considered Goudot's *Herrania* to constitute merely a section of *Theobroma*, which genus he divided into the two sections: *Herrania* and *Eutheobroma*. Bernoulli (Uebersicht der bis jetzt bekannten Arten von *Theobroma*. 4. 1871), on the contrary, had divided *Theobroma* into four sections but kept *Herrania* as a distinct genus, stating, ". . . *Theobroma* ab *Herrania* Goudot genere proxime affini differt praecipue habitu, foliisque integris nec digitatim quinque- sexfoliolatis."

The general tendency in recent years has been to keep *Herrania* and *Theobroma* as distinct genera. Cook (Contr. U.S. Nat. Herb. **17**: 616. 1916), for example, followed this course. Cheesman (The economic botany of cacao. Suppl. Trop. Agric. 1. 1932) pointed to *Herrania* and *Guazuma* as the nearest relatives of *Theobroma*. Chevalier (Révision du genre *Theobroma* d'après l'Herbier du Museum National d'Histoire Naturelle de Paris. Rev. Bot. Appl. Agric. Trop. **26**: 265. 1946) excluded *Herrania* from his treatment of *Theobroma*. A recent morphological and taxonomic study of *Guazuma* (Freytag, G. F., A revision of the genus *Guazuma*. Ceiba **1**: 193 ff. 1951) offers data which very convincingly support the separation of *Herrania* from *Theobroma*.

A comparative study of the pollen of *Herrania*, *Guazuma*, *Theobroma* and other allied genera, outlined in detail below, has indicated that there are appreciable differences between the pollen of *Herrania* and *Theobroma*.

There is still not complete agreement, however, in the generic interpretation of *Herrania*. In 1940, Ducke (Rodriguesia **4**: 273. 1940) treated *Herrania* as a "subgenus (or section)" of *Theobroma*. A chromosome study of several species of *Theobroma* and *Herrania* carried out by Muñoz (Estudios cromosómicos en el género *Theobroma* L. Unpubl. Thesis. Fac. Inst. Interam. Ciénc. Agríc. Turrialba 30–35. 1948), indicates that the number in both concepts is $2n = 20$. The chromosomes are very similar, but they are generally more slender and more definitely contrasted in *Herrania albiflora*, *H. purpurea* and *H. pulcherrima* (the only three species studied) than in those species of *Theobroma* which were examined. Muñoz feels, but is not entirely certain, that *Herrania* should be treated as a section of *Theobroma*.

Most recently, Ducke (As espécies brasileiras do gênero *Theobroma* L. Bol. Técn. Instit. Agron. Norte **28**: 3–20. 1953) has reiterated his belief that *Herrania* and *Theobroma* should be treated as a single genus.

It is pertinent to this discussion that recently *Theobroma* and *Herrania* have been shown experimentally to be very closely allied. Ing. Agron. Addison, geneticist at the Instituto Agronômico do Norte in Belém do Pará, Brazil, successfully pollinated *Theobroma Cacao* with *Herrania Mariae*, but the embryos failed to develop (Addison, G. O'N., & R. M. Tavares, Observações sobre as espécies do gênero *Theobroma* que ocorrem na Amazônia. Bol. Técn. Instit. Agron. Norte **25**: 1951).

Van Hall (Cacao. ed. 1. 1914; and ed. 2. 1932) treated *Herrania* as a section of *Theobroma*. On the other hand, Pound (Cacao and witchbroom disease (*Marasmius perniciosus*) of South America. 47 ff. 1938), while not definitely committing himself, outlined in very great detail the characteristics of *Herrania* and pointed out the important differences between *Herrania* and *Theobroma*.

The following key (adapted primarily from Schumann's key to his sections *Herrania* and *Eutheobroma* of the genus *Theobroma*) sets forth the gross characters by which *Herrania* may be separated from *Theobroma*.

A. Arbores parvae et graciles. Folia quinque- ad novem-digitata. Petalorum ligulae lineares vel filiformes, comparate longissimae, cucullum multo

superantes, in alabastro circinnato-involutae. Calyx usualiter 3-fidus. Fructus saepissimae conspicue costatus, pericarpio vulgo aliquid crassulento. ..... **Herrania.**

AA. Arbores. Folia integra. Petalorum ligulae, duplo vel triplo cucullum superantes, vel breviores, in alabrastro reflexa vel erecta. Calyx usualiter 5-fidus. Fructus saepe obscure costatus vel sublaevis, pericarpio ut videtur saepius sicco et duro. ..... **Theobroma.**

Herrania Goudot, Ann. Sci. Nat. III. **2**: 230. *t. 5.* 1844; Walpers, Rep. **5**: 111. 1845–46; Endl. Gen. Pl. Suppl. **4**: 62. 1850; Karst. Linnaea **28**: 446. 1856; Tr. et Planch. Prodr. Fl. Novo-Granat. 209. 1862; Benth. et Hook. Gen. Pl. **1**: 225. 1862; Walpers, Ann. Bot. Syst. **7**: 225. 1862, **7**: 430. 1868; Baill. Hist. Pl. **4**: 131. 1873, Dict. Bot. **3**: 49. 1891.

Lightia Schomb. Rep. Brit. Assoc. Adv. Sci. **2**: 71. 1844. Non *Lightia* Schomb. Linnaea **20**: 757. 1847.

Brotobroma Karst. et Tr. ex Tr. Nuev. jén. y esp. plant. fl. Neo-Granad. 11. 1854.

Type species: *Herrania albiflora* Goudot.

General distribution: From Costa Rica down the Andes to Peru, along the Pacific coast of Colombia and Ecuador, across Venezuela and the Guianas and in the Amazonian basin of Brazil, Colombia, Peru and, probably, Bolivia.

Original description: Calyx 3-partitus, coloratus, deciduus, laciniis aequalibus concavis; aestivatio valvata. Corolla 5-petala, hypogyna, cucullato-concava, apice inflexo in ligulam linearem, ante anthesin concolutam, producta. Androphorum 5-fidum, carnosum, glabrum; laciniis sterilibus cum petalis alternantibus suprene in appendicem erectam vel reflexam dilatatis; laciniis fertilibus longitrorsum adnatis, petalis oppositis, brevioribus, singulis, 3-andris, antheris ovatis didymis. Stylus cylindraceus. Stigmata 5, teretiuscula, obtusa. Ovarium 5-gonum, 5-loculare sessile, disco hypogyno destitutum. Ovula anatropa in singulo loculo anguloque centrali 1-seriata, horizontalia. Fructus ovato-oblongus, costatus, basi et apice subacuminatus, coriaceo-lignosus, indehiscens. Semina in pulpa nidulantia, ovata, angulata, testa pergamacea venosa. Embryo cotyledonibus crassis, hinc convexis, inde planis, radicula brevissima.

Small trees. Leaves unusually large, digitate, 4–9-foliolate. Flowers cauline, fasciculate. Calyx 3–5-fid; sepals more or less divided, valvate in the bud. Corolla 5-parted; petals hypogynous, cucullate-concave, apically inflexed, with a linear or filiform ligule which, before anthesis, is circinnate-involute. Androphore 5-fid, fleshy, glabrous; sterile segments alternate with the petals, enlarged above into erect or reflexed, ovate-lanceolate or linear, petaloid staminodes; fertile segments 1–4(mostly 3)-antheriferous, anthers short-stipitate, with diverging, didymous locules. Ovary sessile, 5-locular, the lower with many anatropous ovules. Style filiform, cylindrical. Stigmas 5, rather terete, obtuse. Fruit ovate-oblong, costate, apically usually subacuminate or acuminate, toughly coriaceous,

indehiscent. Seeds enclosed in a pulp, flattened-ovate, angulate, with a papery testa, exalbuminous; cotyledons thick, sometimes flat, with a very short radicle. Chromosomes: $2n = 20$ (in three species studied).

In his "Woods of northeastern Peru" (Field Mus. Nat. Hist. Bot. Ser. 15: 323–324. 1936), Llewelyn Williams has published what appears to be the only detailed description of the wood of *Herrania*. Williams cited five collections which were used as a basis for this description and referred all of the collections to "*Theobroma Mariae*." I have found that they represent *Herrania nitida*. Until wood samples are collected in exact correlation with herbarium specimens from many areas and for numerous species, an understanding of specific differences in the wood of *Herrania* cannot be appreciated. For this reason, Williams' description of *Herrania nitida* must serve as a guide to the wood structure of the whole genus.

Sapwood pale pink; heartwood pinkish brown. Wood has no distinctive odor or taste; straight- or wavy-grained, coarse-textured; light in weight and soft; requires a sharp knife to cut smoothly across grain; perishable. Growth rings absent or present. Parenchyma indistinct. Pores fairly small or very small; not numerous and well-scattered; solitary or in radial multiples of 2–3. Vessel lines fairly long, not prominent, but discernible to unaided eye. Rays coarse, lighter-colored than background, sometimes wavy, and conspicuous on cross section; darker than background and fairly distinct on tangential; of darker color than adjacent elements and conspicuous on radial surface. Pith light or dark greyish brown.

The examination of the pollen grains of *Herrania*, to the best of my knowledge the first which has been made, was carried out by Dr. Theodor van der Hammen of the Colombian Servicio Geológico Nacional. Pollen of *Herrania tomentella* was analyzed. All terms are used in accordance with Iverson and Troels-Smith's nomenclature proposed in 1950.

Herrania tomentella R. E. Schult. Pollen collection Serv. Geol. Nac. #IV 86. Collection Col. 34377.

Pollen grains: tricolporate, reticulate, subsphaeroidal; granulae of the muri visible but not separated. Lumina of reticulum irregular of size, rather large, polygonal, smaller near the colpae. In the lumina, rather faint granulae are visible. Colpae clear, edges separated; pores clear, without ectexine elements; sometimes indications of small transversal furrows. Magnitudo pollinis: media (28–33 μ). Magnitudo luminum: meso-macro (2–4.7 μ) and smaller. Index pollinis: subsphaeroidea (1–1.12); ('*prolate sphaeroidal*' of Erdtman). Index areae poli: middle (0.30–0.35). Index exinae: middle (0.05–0.08).

Van der Hammen reports further that *Theobroma*, *Guazuma*, *Sterculia* and *Herrania* have tricolporate and reticulate pollen grains but that the grains of *Waltheria* and *Helicteres* are of different types. A comparison of the four genera with tricolporate and reticulate grains leads to the really unexpected conclusion that, insofar as pollen morphology is concerned, there is no evidence that *Herrania* and *Theobroma* are very closely allied. On the contrary, the pollen grains of *Theobroma* resemble those of *Guazuma*

even more than they do those of *Herrania*. Van der Hammen compares the grains of *Theobroma Cacao* and of *Herrania tomentella* as follows: "The grains of *Theobroma Cacao* are subsphaeroidal ('*oblate sphaeroidal*' of Erdtman); index pollinis ± 0.8–0.9; magnitudo pollinis ± 22 μ. The polar area is relatively much larger than that of *Herrania*, the colpae are very narrow, unclear and short. Pores are small and not very clear; lumina of ret much smaller than those of *Herrania* (greatest size measured 1–1.75 μ), and more regular. Exine (including sculpture) relatively thicker than those of *Herrania*."

A most careful and detailed chemical analysis of the seeds of *Herrania* has been made by MacLean (MacLean, J. A. R., Oil-bearing seeds of possible economic importance to West Africa. Nature 169: 589. April 5, 1952). The material studied was reported to be referable to *Herrania balaënsis* and *H. Mariae*, but unfortunately no voucher specimens were cited for checking, and the specific identifications are open to doubt. The plants were introduced from Trinidad to West Africa in 1944. The photographs published on pages 589 and 590 would suggest that one of the species analyzed (probably the one called *Herrania Mariae*) was *H. nitida*.

MacLean reported a very high oil content (up to 66.1%) of the seeds, and it is suggested that optimum cultural conditions might improve this figure. He found that the "percentage of total alkaloids is approximately one-third that of Amelonado beans, and the theobromine-caffeine ratio is reversed." The caffeine values were found to be comparable with the lower limit of range for coffee beans and kola nuts, with values greater than 1% being obtained on two occasions. Freshly extracted fat from *Herrania* seeds is liquid at 25–29°C with an odor resembling that of linseed oil; its specific gravity is 0.93–0.94; and its unsaponifiable matter is less than 1%. The figure for reducing sugars (0.4%) is four times that of Amelonado beans. The iodine values varied from 39 to 47, and the saponification value ran from 203 to 206. The percentage of free fatty acids in the oil ranged from 2.3 to 2.8 The composition of the oil was found to be 18–26% linoleic, 2–7% oleic and 74–76% of saturated acids.

Herrania comprises two groups of species which are sufficiently well marked one from the other to permit their segregation into sections. These two sections are not only distinct in the morphology of the flower; they also fall naturally into two distinct, though overlapping, geographical areas.

Sect. **Herrania**

Calyx patelliformis, sepalis media pro parte connatis. Subgeneris typus: *Herrania albiflora* Goudot.

Sect. **Subcymbicalyx** R. E. Schultes, sect. nov.

Calyx subcymbiformis, sepalis plerumque fere usque ad basim liberis. Subgeneris typus: *Herrania nitida* (Poepp.) R. E. Schultes.

The characters upon which these concepts are founded serve for the

first dichotomy in the following key to the species. *Herrania albiflora*, *H. purpurea* and *H. umbratica* are the only species with the curious patelliform calyx. Their flowers, because of this condition, have a completely different appearance from those of all other species: the patelliform calyx lends a "closed" or compact appearance to the flower, whereas the subcymbiform condition allows for a greater expansion of the petals and their ligules and the staminodes. Furthermore, the ligules of *Herrania albiflora*, *H. purpurea* and *H. umbratica* are extremely short, whilst those of all other species are longer — with the single exception of *H. breviligulata*, very much longer.

The species of the section *Herrania* are confined to Middle America and the northernmost regions of Colombia in South America. Those of *Subcymbicalyx* extend over the whole northern half of South America, in northern Colombia overlapping the area occupied by the three species of Sect. *Herrania*.

Although, at the present state of our understanding of the genus, it is rather difficult to form any well founded phylogenetic picture, the patelliform calyx would appear to me to represent a derived condition and the subcymbiform calyx, conversely, a primitive condition in *Herrania*.

Clavis Specierum Herraniae

A. Calyx patelliformis. Sepala medio pro parte connata. Ligulae usque ad 20 mm. longae. Sect. Herrania.
  B. Petala, ligulae et staminodia alba. Sepala usque ad 7 mm. longa. ..... 1. *H. albiflora.*
  BB. Petala, ligulae et staminodia purpurea vel sanguinea. Sepala 12 mm. longa vel longiora.
    C. Ligulae usque ad 15 mm. longae. Capsulae costae valde inaequales, aliquid tenues, distantes. Fructus usque ad 9 cm. longus. ..... 15. *H. purpurea.*
    CC. Ligulae 19 mm. longae vel longiores. Capsulae costae quasi aequales, crassissimae, non distantes. Fructus 11 cm. longus vel longior. ..... 17. *H. umbratica.*

AA. Calyx subcymbiformis. Sepala plerumque fere usque ad basim libera. Ligulae 25 mm. longae vel longiores. Sect. Subcymbicalyx.
  D. Foliola profunde incisa vel lobata.
    E. Foliola grosse et regulariter pinnatisecta; lobulis anguste triangulari-lanceolatis, acutissimis; lamina subtus densissime et molliter stellato-tomentosa, usque ad 60 cm. longa. Ligulae 180 mm. longae. Capsula maturitate fusco-rubescens; costis longitudinalibus bene conspicui et sine costis transversalibus prominentibus. .... 9. *H. laciniifolia.*
    EE. Foliola maxime grossissime sed irregulariter pinnatilobata; lobis late triangularibus, acutis lamina subtus aspera, stellatis cum pilis, usque ad 80 cm. longa. Ligulae 85 mm. longae. Capsula maturitate ochracea (?); costis transversalibus bene prominentibus. ..... 10. *H. lemniscata.*
  DD. Foliola integra vel leviter dentato-sinuata vel undulata.
    F. Ligulae 25–35 mm. longae. Foliola subtus cum indumento subcinereo-velutino. ..... 3. *H. breviligulata.*

FF. Ligulae 60 mm. longae vel longiores. Foliola subtus glabra vel cum indumento aspero vel molle, sed numquam velutino.

G. Foliola glabra vel subtus sparsissime aspero-tomentulosa. ..... 12. *H. nitida.*

GG. Foliola variabiliter sed molliter pilosa vel tomentosa.

H. Foliola valde et regulariter sinuata.

I. Capsula costis quinque longitudinalibus rectis armata et laevis vel transverse striatofibrosa; maturitate flava. Staminodia quam 17 mm. longiora, apice acuta vel conspicue trifida.

J. Foliola maxima, 45–60 cm. longa vel saepissime longior × 19–35 cm. lata, latissime lanceolato-ovata, ½ lata duplo longior quam latior, apicem versus grossiuscule sinuata, dentibus 5–9 cm. distantibus. Petala et ligulae rufo-purpurea. Ligulae 2–3 mm. latae. Staminodia apice trifida. ..... 14. *H. pulcherrima.*

JJ. Foliola minor, usque ad 60 cm. longa sed saepissime brevior × 10–15 cm. lata, anguste lanceolato-elliptica, quadruplo longior quam latior, dentibus 2–4 (rarenter 5) cm. distantibus. Petala et ligulae albicantes, ligulae minores quam 2 mm. latae. Staminodia apice acuta.

K. Foliola usque ad 30 cm. longa × 11 cm. lata. Sepala inaequalia; majora 15–16 mm. × 15 mm.; minora 10 mm. × 6 mm. Petala 9 mm. × 7 mm. Staminodia lanceolato-elliptica, 22 mm. × 6 mm. ..... 8. *H. kofanorum.*

KK. Foliola usque ad. 60 cm. longa sed vulgo brevior × 15 cm. lata. Sepala subaequalia, 14 mm. Petala 8 mm. × 5 mm. Staminodia elliptica, 18 mm. × 8 mm. ..... 2. *H. balaënsis.*

II. Capsula costis quinque longitudinalibus rectis armata sed etiam transverse bene costata, in junctionibus costarum longitudinalium et transversalium projectionibus spiniformibus longis, mollibus et crassis productis; maturitate sanguinea vel rarenter flava. Staminodia usque ad 14 mm. longa, apice valde obtusa. ..... 4. *H. Camargoana.*

HH. Foliola normaliter integra, subintegra vel apicem versus plus minusve sinuosa.

L. Foliola lanceolato-oblonga, usque ad 60 cm. longa × 22 cm. lata, basi longe et sensim attenuato-decurrentia. Petioli 45–60 cm. longi.

M. Capsulae costae tenues, late cultriformes, principaliter costa versus pilis urticantibus armatae, tactu asperae; capsula alibi glabra vel glabrescens. ..... 5. *H. Cuatrecasana.*

MM. Capsulae costae crassae, hebetato-rotundatae, sine pilis urticantibus; capsula omnino molliter indumento stellato-velutino armata.

N. Capsula ovoidea, apice breviter cuspidata vel subrotundata, costis minoribus, primariis usque ad 2 mm. altis, secundariis haud prominentibus. ..... 7. *H. kanukuensis.*

NN. Capsula ellipsoidea, apice obtusa vel attenuata, costis majoribus, primariis usque ad 8 mm. altis, secundariis usque ad 3–5 mm. altis.

O. Capsula 10–12 cm. longa, 4–5 cm. in diametro, apice longe et sensim attenuata, cum costis hebetatis crassissimis, non bene distantibus, inter costas prominenter fibroso-rugosa. Ligulae usque ad 90–100 mm. longae. Staminodia apice leviter trifida. .... 13. *H. nycterodendron.*

OO. Capsula 9 cm. longa, 4 cm. in diametro, apice vulgo obtusa, cum costis hebetatis crassis, bene distantibus, inter costas paullo et leviter fibroso-rugosa. Ligulae usque ad 70 mm. longae. Staminodia apice acuta. ..... 16. *H. tomentella.*

LL. Foliola obovato-oblonga vel subrhomboidea, usque ad 31 cm. longa × 12 cm. lata, basi aliquid attenuata vel quasi cuneata. Petioli plus minusve 30 cm. longi.

P. Foliola obovato-oblonga, vulgo 35 cm. longa vel minora. Sepala aequalia vel subaequalia, 21 mm. longa × 12 mm. lata, intus subdense ferrugineo-pilosa. Petala 11–12 mm. × 5–6 mm. Ligulae atrosanguineae vel atro-purpureae, 100 mm. longae, 2 mm. latae. Staminodia lanceolata, apice acutissima, integra 12–15 mm. × 5 mm. ..... 6. *H. Dugandii.*

PP. Foliola rhomboideo-obovata, vulgo 30–35 cm. longa. Sepala valde inaequalia; majora 12–15 mm. longa × 6–10 mm. lata; minora 11–13 mm. × 11–12 mm., intus glabra vel minutissime pilosa. Petala 7–9 mm. × 6–8 mm. Ligulae albicantes, 75–100 mm. longae, usque ad 1 mm. latae. Staminodia lanceolato-elliptica, apice obtusa et saepe indentato-mucronata vel serrata, aliquid sinuato-undulata, 20 mm. × 6–7 mm. ..... 11. *H. Mariae.*

1. **Herrania albiflora** Goudot, Ann. Sci. Nat. Paris III. 2: 230. *t. 5, fig. 1–10.* 1844; Tr. et Planch. Prodr. Fl. Novo-Granat. 1: 209. 1862; Schultes, Caldasia 2: 325. 1944.

Theobroma albiflorum (Goudot) De Wildeman, Pl. Trop. Grande Cult. 90. 1902.

DISTRIBUTION: Northern sector of the Magdalena basin in Colombia and in westernmost Venezuela.

Small tree up to 16 feet tall consisting of several round, simple or (rarely) branching trunks, 11–14 cm. in diameter, with a greyish bark. Leaves grouped at the apex of the trunk, digitate, stipulate, 5–6-foliolate. Branches densely and minutely ferruginous-tomentulous, probably becoming almost glabrous. Petioles terete, densely and minutely ferruginous-villose, somewhat dilated at the base, as long as the leaves, conspicuously striate-sulcate, up to 45 cm. long, 4–6 mm. in diameter. Stipules conspicu-

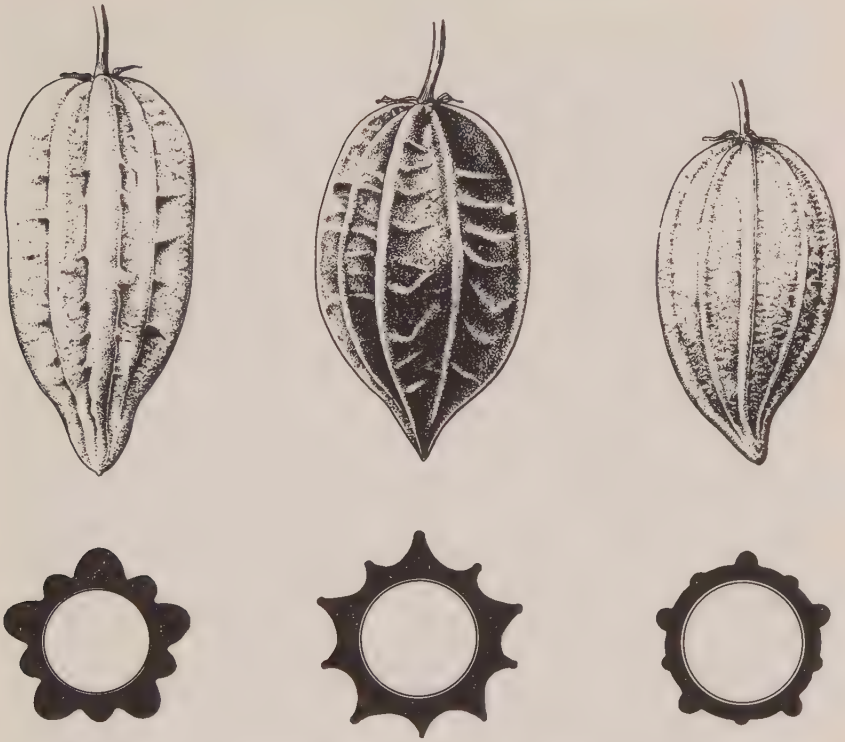


FIG. 1. Fruits of *Herrania nycterodendron*, *H. Mariae*, and *H. kanukuensis* (left to right) with schematic cross sections.

ous, linear, entire, acute, caducous, ferruginous, 50 mm. long, 3–4 mm. wide. Leaflets lanceolate-obovate, acuminate, basally long-attenuate-decurrent, very shortly petiolulate (petiolule strong, 3–4 mm. long), marginally entire, thin-chartaceous, 20–60 cm. (usually 50 cm.) long, 9–15 cm. wide, dark green and glabrous above, pale green and almost glabrous, or with extremely remote and microscopic stellate hairs, beneath; the veins of both surfaces prominent, clothed with ferruginous, minute and weak puberulence. Inflorescence fasciculate, few-flowered (5 or 6 flowers). Flowers subglobose, 15 mm. in diameter, borne in contracted racemes on the lower and middle part of the trunk, white, pedicellate. Pedicels very short, cylindric, fulvous-tomentulose, subtended at the base by a minute, very densely fulvous-tomentulose, linear bract. Flower buds small, globose, tomentose. Calyx patelliform. Sepals 3, subequal, connate half their length, rotund-ovate, rounded, marginally entire, yellowish white, externally densely stellate-villose, internally glabrous, about 7 mm. long, 6 mm. wide. Petals 5, very broadly rotund-ovate, cucullate, glabrous near the apex, thick-membranaceous, somewhat muricate-granulose on both surfaces, 5 mm. long, 4 mm. wide, longitudinally striate-veined, internally with conspicuous veins, ligulate, white. Ligules linear, reflexed, white, glabrous,

membranaceous, with 6 or 7 brownish nerves, up to 2 cm. (usually shorter) long, less than 1 mm. wide at the base. Stamen tube 5-fid, alternately 2- and 3-antheriferous with short, simple, free filaments and 2-locular, divergent, longitudinally dehiscent anthers. Staminodes petaloid, very broadly ovate, acute, reflexed, 6 mm. long, 5 mm. wide, densely muricate-granulose on both sides, marginally entire. Pistil short, more or less 1.5 mm. long. Style linear, erect, glabrous with a 5-parted stigma. Ovary sessile, subglobose, pilose, 1.3 × 1 mm. Fruits capsular, oblong, apically short-acuminate, the tip somewhat rounded, hispid, 10-costate, yellow when ripe, 11–14 cm. long. Seeds 30–40, irregular, compressed, enveloped in a white, mucilaginous pulp, slightly acid, covered with an internal membranous tegument and an internal pellicle, coriaceous and exteriorly rugose. Embryo brown, with 2 thick, unequal, rarely folded cotyledons and a very short radicle.

Colombia. [No definite locality, probably near Mariquita], *Exped. Bot. Mutisii Novae-Granat. 3759.* ANTIOQUIA: Vuelta de Acuña, Río Magdalena [leaves only referable to *H. albiflora*], *Pennell 3799*; opposite Boca Carare, alt. 125 m., *Pennell 3832.* BOLIVAR: Bojorque [Bohórquez], Río Magdalena, *Bonpland 1580*; Norosi-Tiquisio Trail, Lands of Loba, alt. 150–600 m., *Curran 135*; Boca Verde, Río Sinú, alt. 100–300 m., *Pennell 4208.* CUNDINAMARCA: Muzo, *Goudot s.n.* (Type); Río Guaco, near Muzo, *Purdie s.n.* SUR DE SANTANDER: vicinity of Puerto Berrio, between Carare and Magdalena Rivers, alt. 100–700 m., *Haught 1598.* **Venezuela.** ZULIA: vicinity of Perija, *Tejera 268.* **Trinidad.** Royal Botanic Gardens, Port-of-Spain, *No Collector Cited*; *Bailey s.n.*; Imperial College of Tropical Agriculture, Diego Martin Estate, *Schultes 18639.*

Herrania albiflora is very closely allied to *H. purpurea* from which it can be distinguished by its white or cream-colored flowers. There are also other differences: the sepals of *Herrania albiflora* are usually much smaller than those of *H. purpurea*; the stipules of the former are longer than those of the latter species; the leaflets of *H. albiflora* are lanceolate-obovate, whereas those of *H. purpurea* tend to be obovate-oblong; and the petals of the former species are very broadly rotund-ovate, 5 mm. × 4 mm., whilst those of the latter are obovate, 8 mm. × 8 mm.

The habit and general floral structure of *Herrania albiflora*, *H. purpurea* and *H. umbratica* are strikingly similar. These species alone in the genus have a patelliform calyx, which gives the flower a completely different appearance from the usual cymbiform calyx. The ligules in these three species are likewise similar in structure and are under 20 mm. in length.

Purdie s. n., one of the earliest collections of the species, was identified as *Herrania albiflora* at Kew by Planchon, who annotated the sheet, a topotype. The report of the collector of this specimen relative to his having seen "several hundreds of fruits" on a cultivated tree of *Herrania albiflora* must be recognized as an exaggeration. Although fruits are often very numerous in most of the species of *Herrania*, I have never met any condition which would indicate "hundreds of fruits".

It has always been presumed that the type of *Herrania albiflora*, the

type-species of the genus, was preserved in the herbarium at Paris, but in June, 1950, I found Goudot material at Geneva which may very well be the type of *Herrania albiflora*. In Geneva, there are three sheets representing the Goudot collection of this species, all labelled, in his handwriting: "C. N. 1 *Herrania albiflora* mihi. Annales Sc. Nat. 1844. Muzo." One sheet has several very young and membranaceous leaves and an envelope in which there are fragments of a fruit belonging possibly to an annonaceous plant and which, by some error, have been associated with the *Herrania* collection. Another sheet has a complete and mature leaf. The third sheet has three envelopes: one contains several seeds of *Herrania albiflora*; another has a few flowers and a very young capsule; the third has a flower completely dissected, with the parts glued flat to the envelope. An examination of these floral parts and of Goudot's description and drawing of *Herrania albiflora* leads me to the conclusion that, at least for the flowers and fruits, the Geneva material is the type of the species and genus. As to how has it been possible for Goudot type material to find its way to Geneva one cannot be certain. There are, of course, many Goudot collections in the Delessert Herbarium (cf. A. Lasègue, Musée Botanique de M. Benjamin Delessert. 471. 1845).

It may be of interest to note that a comparison of the Goudot floral dissection with the description of *Herrania albiflora* has uncovered several minor discrepancies or omissions. The sepals, described as glabrous within, have a very minute and sparse puberulence on the lower portion of the inner surface; and the petals are extremely muricate-granulose externally, as are also the very short ligules in the basal portion near their junction with the petal.

One of the Mutis plates in Madrid, executed by the Colombian botanical artist Francisco Javier Matíz, represents a fruiting and flowering branch of *Herrania albiflora*. Not only are ripe and unripe fruits shown in excellent detail, but a large number of flowers are depicted so painstakingly that it is clear that Mutis and his colleagues could, so long ago, differentiate between the patelliform calyx of *Herrania albiflora* and the subcymbiform calyx of the other species illustrated. No foliage is drawn on the plate of *Herrania albiflora*. Triana correctly annotated this plate as "*Herrania albiflora* Goudot."

In the Mutis collection of plants in Madrid, there is a sterile collection of leaves, misidentified as "*Theobroma Mariae*," which represent *Herrania albiflora*. They undoubtedly belong to the plant the flowers and fruits of which are portrayed on the Mutis plate of *Herrania albiflora*.

Van Hall (Cacao. ed. 2. 74. 1932) claims that "according to Goudot, who collected this species near Muzo (Colombia), the seeds are mixed with those of the commercial cacao for home use; they are said to improve the taste of the chocolate." He credits Goudot with the report that "the seeds are also used, unmixed, for the preparation of a very bitter product which is used by the population as a febrifuge".

Herrania albiflora is generally recognized as a cacao-relative. Hart (Cacao. 13. 1911) reports that "*Herrania albiflora* and *Pachira insignis*

have both been sent to the author as 'wild' cacao, but neither of these trees has anything in common with *Theobroma Cacao* and neither of them produces saleable samples".

1a. **Herrania albiflora** Goudot f. **titanica** R. E. Schultes, Caldasia 3(15): 442. *t. pag. 443.* 1945.

DISTRIBUTION: Western or Magdalena slope of the eastern Cordillera in the Departamento del Sur de Santander, Colombia.

Usually a robust tree up to 30 feet in height, differing from *Herrania albiflora* principally in having much larger leaves and flowers.

Colombia. SUR DE SANTANDER: Carare, Landazuri alt. 1000 m., *Richter s.n.* (Type); vicinity of Barranca Bermeja, Magdalena Valley, between Sogamosa and Colorado Rivers, alt. 100–150 m., *Haught 1490.*

The collection *L. Richter s. n.* seems to present clear evidence that there exists a very large variant of *Herrania albiflora*, which may probably best be treated as a distinct *forma*. The leaves are not only very large for the species, but, in *Richter s. n.*, the entire plant is exceptionally robust for the genus, measuring up to 10 meters in height. The height of the plant from which *Haught 1490* came is not given, but the collector notes that it was "a small tree;" this would seem to indicate, in the case of such a meticulous collector as Haught, that it was *not*, as in nearly all the species known, a "treelet." The leaves of *Haught 1490* are much larger than in the Richter collection.

I have found that within a species of *Herrania* the size of the leaves is more or less standard, regardless of whether it grows in shaded forest or open pasture. This causes me to feel that the unusual size of the leaves of *Herrania albiflora* f. *titanica* does not represent a mere ecological variant.

Vegatatively, the new form is almost indistinguishable from *Herrania umbratica* of the same general region, but there are important differences in the fruits (Caldasia 2: 261–264. *tt. 2, b, c, d.* 1943). It is unfortunate that, except for the drawing which accompanies the original description, we know very little of the fruit of *Herrania albiflora*. The capsule of *Herrania albiflora* f. *titanica* is similar to that of *H. purpurea*, being somewhat intermediate between *H. purpurea* and *H. umbratica*. It measures 12.5–14 cm. in length and 5–5.5 cm. in diameter and has low, rounded unequal ribs; the apex is acuminate.

Richter informed me that he collected a few dried flowers from the base of the type of *Herrania albiflora* f. *titanica* and that they showed evidence of having been white or yellowish in life. Unfortunately, these were lost in shipment. The color of the flower in *Haught 1490* is uncertain, for the label bears no note in this respect. But with *Haught 1598* (a collection representing *Herrania albiflora*) is a note stating: "a small cauliflorous tree, cf. *1490,* from which this differs in having white flowers."

2. **Herrania balaënsis** Preuss, Exped. Centr.- und Süd-Amerika (1899–

1901). 253. *t. 7.* 1901; Bull. Soc. Études Col. Ann. 9(4): 220. *t. pag. 221. 256, fig. 1–8.* 1902 (non accurate titulata).

Theobroma balaënsis (Preuss) De Wildeman,[2] Pl. Trop. Grande Cult. 89. 1902.

Small tree up to 25 feet in height, with a slender, simple, very straight cylindrical trunk about 15 cm. in diameter at the base. Leaves arranged at the apex of the trunk, digitate, usually 7-foliolate, petiolate. Petioles terete, sulcate, very densely ferruginous-tomentose, up to 30 cm. long, about 5 mm. in diameter. Leaflets unequal, lanceolate-elliptic, marginally conspicuously sinuate, apically strongly acuminate, basally long attenuate-decurrent, sessile, firmly chartaceous, up to 60 cm. long, 15 cm. wide; leaf blade dark green and glabrous or subglabrous (microscopically scabridulous with minute stellate puberulence) above, brownish green and very densely and softly ferruginous-stellate-pilose beneath; the veins prominent and brown-tomentose on both sides, especially beneath. Inflorescence fasciculate, many-flowered (12–15 flowers), on the lower and middle portions of the trunk. Pedicels robust, densely greyish stellate-pilose, 8–9 mm. long, 1–1.5 mm. in diameter, subtended at the base by a minute, very densely stellate-pilose, linear bract. Calyx subcymbiform. Sepals 3, subequal, externally reddish brown, internally deep purple, lanceolate-elliptic, apically subacute, marginally entire, very densely muricate-papillose or granulose, 14 mm. long, 6 mm. wide. Petals 5, very broadly ovate, strongly cucullate, 8 mm. long, 5 mm. wide, whitish with 8–10 purplish veins, densely muricate-papillose, sparsely stellate-pilosiusculous externally, papillose, glabrous internally, ligulate. Ligules of the petals white and rose-colored, filiform, glabrous, very minutely granulose, membranaceous, 100 mm. long, less than 2 mm. wide. Staminal tube 5-parted; stamens alternately 2- and 3-antheriferous with relatively long, simple, glabrous filaments and 2-locular, divergent, longitudinally dehiscent anthers. Staminodes 5, petaloid, reflexed, membranaceous, elliptic, apically acute, marginally entire, glabrous, minutely and densely muricate-granulose on both sides, probably purplish red, 17–18 mm. long, 7–8 mm. wide. Pistil about 5 mm. long. Style linear, erect, glabrous with a 5-parted stigma. Ovary sessile, subglobose, 5-ribbed, densely white-pilose, 1.8–2 mm. in diameter, 3 mm. long. Fruit elongate-ovoid, the apex long-acuminate, 10-costate with 5 primary and 5 secondary ribs, olive-green when young, yellow-green and hispid when ripe, about 14 cm. long.

Ecuador. Río de Peripa, *Andre K26*; El Recreo, *Eggers 14362*; Balao, *Eggers 14362*. **Trinidad.** CULTIVATED: Imperial College of Tropical Agriculture, Diego Martin Estate, *Schultes 18638*.

Herrania balaënsis appears to be most closely allied to *H. kofanorum*. This relationship will be discussed under *Herrania kofanorum*. This species also resembles *H. Dugandii*, from which it differs in being very

[2] This combination, as "Theobroma balonsis," has recently been made by Llano Gómez (p. 18, Cultivo del cacao. Publ. Min. Econ. Nac. Bogotá. 1947), who apparently was unaware of the earlier publication.

much larger in its vegetative parts; in having conspicuously sinuate (instead of nearly entire) leaflets; in having much smaller sepals which are externally granulose (instead of stellate-pilose) and smaller petals which are whitish (instead of red-purple) and sparsely covered with a stellate puberulence; in having much larger staminodes; and in several other minor respects.

Herrania balaënsis has a type of fruit which immediately sets it apart from most other species. The structure of the fruit, according to the drawing of the capsule which was published with the original description, is similar to that of an unrelated species, *Herrania kanukuensis*.

The specific epithet *balaënsis* refers to the locality from which the type was taken.

Llano Gómez (loc. cit. 18) reported that this species is cultivated to some extent in Ecuador, but whether this refers to the toleration of the plant as a wild intruder in plantings or to actual cultivation is not clear. It seems probable that *Herrania balaënsis* is actively cultivated.

3. **Herrania breviligulata** R. E. Schultes, Caldasia 1: 19–24. *t. pag. 21, figs. 1–4, t. pag. 24, fig. 5.* 1942.

DISTRIBUTION: Upper reaches of the Putumayo River, Colombia, and adjacent Ecuador.

Small, slender, graceful tree up to about 15 feet in height. Trunk erect, branching near the apex, terete, 6–7 cm. in diameter, with ashy-brown rimose-scrobiculate bark. Branches apparently tomentose, becoming glabrous. Branchlets densely villose, with rust-colored hairs, becoming almost glabrous. Leaves large, 4- or 5-digitate, very long-petiolate. Petioles terete, basally slightly swollen, subferruginous, tomentulose, up to 46 cm. long, about 0.5 cm. in diameter. Leaflets sessile, unequal, lanceolate-oblong, the margin entire, firmly chartaceous or papyraceous, mostly 20–40 cm. long, 6–30 cm. wide, very cuspidate-acute, up to 3 cm. long-decurrent-attenuate, puberulent on both surfaces but especially so beneath; above light green, very sparsely and minutely stellate-pubescent with white hairs, beneath pale green, densely and velvety stellate-villose-sericeous; the veins prominently elevated and brown-tomentose on both surfaces but especially so beneath. Inflorescence fasciculate, 5–8-flowered. Flowers cauline, in contracted racemes from the upper portion of the trunk, dark crimson-purple, pedicellate. Pedicels about 5–7 cm. long, very densely brown-tomentose, articulate, basally subtended by a short, linear, very densely brown-tomentose bract 1–1.5 mm. long. Bud globose, 4–9 mm. in diameter, very densely rusty-villose. Calyx 3-parted, divided almost to the base, subcymbiform. Sepals 3, broadly elliptic-oblong, obtuse, marginally slightly revolute, crimson-purple, 13–14 mm. long, 7–9 mm. wide, internally very sparsely puberulent or glabrescent, externally beset rather densely with long, white, stellate hairs, valvate in the bud. Petals 4, basally sessile, obovate, 6–7 mm. long, 5–6 mm. wide, concave, strongly cucullate, muricate-papillose or granulose on both surfaces but especially so externally,

5-nerved, longitudinally striate-veined, internally with prominent veins, dark crimson-purple, ligulate. Ligules linear, 25–35 mm. long, 1.5–2 mm. wide, hanging, basally slightly and abruptly contracted, apically slightly inrolled in a spiral position, 3-nerved, yellowish-red, with purple nerves, very minutely muricate-papillose or granulose. Staminal tube 5-parted, with stamens alternately 2- and 3-antheriferous and simple, short, free filaments. Staminodes petaloid, dark scarlet, lanceolate-elliptic, acute, margin entire, muricate-granulose on both surfaces, 15 mm. long, 4 mm. wide, crimson-purple. Pistil 2.8 mm. long. Style terete, simple, purplish, with a deeply 5-parted stigma. Ovary sessile, very densely pilose, pale yellow, subglobose, 3 mm. long, 2 mm. wide. Fruit unknown, but said to be pale yellow when ripe.

Colombia. PUTUMAYO: Mocoa, alt. 850 m., *Schultes & Smith 2050* (Type), *Schultes & Cabrera 19082*, *Anglo-Colombian Cacao Collecting Expedition* (*Cope & Holliday*) *78*; Río Caquetá, Puerto Limón, *Schultes & Cabrera 18720*. **Ecuador.** NAPO-PASTAZA: near Archidona, alt. 650 m., *Mexia 7320*.

Herrania breviligulata seems to be closely allied to no other known species of the genus. In some respects it resembles *H. Cuatrecasana* but can be separated from this species readily by having seven (instead of four or five) smaller leaflets with an entire (instead of crenate-denticulate) margin, a more cuneate base and a much softer and denser indumentum on the lower surface; an inflorescence with only six or eight (instead of eighty or ninety) flowers; much smaller buds; pedicels which are 5–7 mm. (instead of 20–30 mm.) long; somewhat smaller sepals and petals; ligules 25–30 mm. (instead of 130 mm.) long; and much smaller staminodes (14 mm. × 4 mm. instead of 25 mm. × 8 mm.) which are apically acute. Both species are known only from the upper reaches of the Putumayo River and adjacent regions, an area which would appear to be one focus of speciation in the genus.

Herrania breviligulata has the shortest ligules known for any of the species with a subcymbiform calyx, a characteristic which is suggested by the specific epithet. It is likewise distinguished from all other known species by the very soft and dense, greyish indumentum which is velvety on the under surface of the leaflets.

The Ecuadorean collection *Mexía 7328* bears the data: "Fruit green, deeply ribbed." I have been able to find only one specimen of this collection (that in the Riksmuseum in Stockholm) and this is without a capsule. The fruit of *Herrania breviligulata*, therefore, remains unknown, Mexía's field notes notwithstanding.

4. **Herrania Camargoana** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 120. *tt. 29, 32.* 1950.

Theobroma Camargoana (R. E. Schultes) Ducke, Bol. Técn. Inst. Agron. Norte **28**: 15. 1953.

DISTRIBUTION: Upper Rio Negro basin in Brazil and Colombia.

Small, slender and graceful tree, usually up to 10 (but sometimes up to 27) feet tall. Trunk erect, sparsely branched or else unbranched near the top, about 4–5 inches in diameter, covered with a black bark. Branches tomentose, but soon glabrous. Branchlets densely villose, ferruginous, subglabrescent. Leaves very large, digitate, 7- to 9-foliolate, very long-petiolate. Petioles terete, strongly constricted at the base, softly golden-ferruginous-tomentellous, up to 60 cm. long, 10 mm. in diameter. Stipules persistent, subulate, very densely tomentellous, up to 3 cm. long. Leaflets sessile, oblanceolate or broadly lanceolate-ovate, slightly erect, unequal, membranaceous-papyraceous, acuminate, basally attenuate, marginally regularly and conspicuously sinuate in the upper half and everywhere armed with cilia-like stellate hairs (up to 1.5 mm. long), 60–75 cm. long, 16–26 cm. wide, asperous above, sparsely pilose with long and single hairs, beneath rather softly tomentellose with long stellate hairs. Inflorescence fasciculate, many-flowered, growing from all parts of the trunk but principally from the lower portions. Pedicels articulate, up to 28 mm. long, 0.8 mm. in diameter. Buds globose, up to 10 mm. in diameter, stellate-pilose. Calyx 3-parted, divided nearly to the base, subcymbiform. Sepals widely elliptic-oblong, subacute, marginally entire, externally dark purple, internally blood-red, mostly 12 mm. long, 8–9 mm. wide, glabrous within, stellate-pilose with rust-colored hairs (up to 1 mm. long) and very minute white hairs without. Petals 5, sessile, obovate-rotund, very strongly concave-cucullate, about 8 mm. long, 6 mm. wide, with 5 dark purple longitudinal nerves as well as finely reticulate nerves, elsewhere yellow, externally conspicuously muricate-verrucose, apically extended into a ligule. Ligules linear, mostly 90 mm. long, at the base 1.7 mm. wide, apically filiform, at the very base blood-red but for the greater part of their length whitish yellow. Staminal tube 5-parted with 2-antheriferous stamens and short free and simple filaments. Ovary ellipsoid, 3.5 mm. long, 2–2.5 mm. in diameter, very densely and coarsely white-pilose. Style terete, simple, yellow, with the stigma apically inconspicuously 5-parted, 3 mm. long. Staminodes conspicuous, rhomboid-elliptic, obtuse, marginally entire, verrucose on both surfaces, ashy purple, 14 mm. long, 5 mm. wide. Fruits numerous, almost globose, or slightly ellipsoid, apically very abruptly long-apiculate (apicule 2–2.5 cm. long), mostly 8–8.5 cm. long, 3.5–4.5 cm. in diameter, basally attenuate, with persistent sepals, longitudinally 10-costate with the primary and secondary ribs almost equal, thin, knife-shaped, irregular in height but for the most part (in life) 5–6 mm. high, transversely irregularly but conspicuously costate with knife-shaped ribs, which are slightly lower or often somewhat higher than the longitudinal ribs, the junction of the longitudinal and transverse ribs prolonged into a softly carnose, mammose or spine-like projection (which is somewhat blunt at the tip) with stinging, stellate hairs in all parts but especially along the ribs; the pericarp thick, usually dark red or blood-red (but sometimes yellow) when ripe; seeds 25, obtusely round-pyramidal, about 9 mm. long $\times$ 11 mm. wide $\times$ 7 mm. thick, imbedded in a white pulp.

Brazil. AMAZONAS: Rio Negro, Serra de São Gabriel, *Schultes & López 9722* (Type); Rio Negro, *Fróes 21468*; Rio Negro, Uaupés (São Gabriel), *Fróes 21540*; summit of Serra de São Gabriel, alt. 100 m., *Schultes & López 8758, 8759, 8762, 8763, 9162, 9619*; Tapurucuara (Santa Isabel), *Schultes & López 8956*; Serra de Uanarí, *Murça Pires 775; Schultes & Murça Pires 8978*; mouth of Rio Xié, *Schultes & López 9205*; Nazaré, *Schultes & López 9240*; Serra Jacamín, *Schultes 9747*; between São Felipe and Karapaná, *Schultes & López 9869*; Rio Padauiary, *Fróes 22673*; Rio Uaupés, between Ipanoré and confluence with Rio Negro, Serra Wabeesee, on left bank below Bela Vista, *Schultes & López 9144* (Type of flowers); *Schultes & Murça Pires 9130*; *Murça Pires 1159*.

Colombia. VAUPES: Caño near north end of Inambú, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 56*; Río Negro, San Felipe and vicinity (below confluence of Río Guainía with Casiquiare), alt. about 600 ft., Caño Marijabo, *Schultes, Baker & Cabrera 18050*; *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 45*.

Restricted apparently to the uppermost Río Negro basin of Brazil and Colombia, *Herrania Camargoana* seems to have as its closest ally the Guianan and Venezuelan *H. lemniscata*. This relationship is strikingly evident when one compares the fruits of the two concepts. Both species have relatively small capsules in which there are transverse ribs nearly as large as the cultriform longitudinal ribs, and soft, pointed mammoid projections at each junction of the longitudinal and transverse ribs. The former species, however, has much longer and more upturned projections than the latter, and would seem, in this as in some other characters, to represent an extreme in the evolution of the genus. There would appear to be a rather easily traceable trend from *Herrania Mariae* through *H. lemniscata* to *H. Camargoana*, on the one hand, and to *H. laciniifolia* on the other.

The coloration of the flowers of *Herrania Camargoana* and *H. lemniscata* is similarly complex and may also indicate a relationship. No other known species of *Herrania* can match these two for complexity of floral coloration. *Herrania Camargoana* has sepals which are dark blood-red externally but scarlet internally; petals which are ashy red or purple with yellowish stripes; staminodes which are ashy purple-maroon with white-yellow patches internally but entirely dark red externally; and ligules, red without and white-yellow within, which are folded or inrolled, so that the red is enclosed and is not seen directly. *Herrania lemniscata* has, according to field notes (*Steyermark 60558*), sepals which are white in the uppermost two-thirds and rose-salmon below, with rose stripes; and staminodes (called "petals" on the label) which are dull yellow with dull rose specks in the lower half.

The shape and size of the leaflets, however, differ strikingly in the two concepts. *Herrania Camargoana* has oblanceolate or broadly lanceolate-ovate leaflets which measure 60–75 cm. in length and 16–26 cm. in width with the upper half regularly and conspicuously sinuate. *Herrania lemniscata* has leaflets which are at least 80 cm. long and 40 cm. wide with the margin very deeply pinnatilobate with usually four irregular and, for

FIG. 2. Crown of *Herrania Camargoana*.

the most part, widely triangular or widely lanceolate-acuminate segments, each up to 18 cm. long and 9–10 cm. wide.

Herrania Camargoana is unusually abundant near the summits of the isolated granitic mountains of the upper Río Negro valley. It has also been found in sandy patches along the banks of the rivers themselves. A search through the Spruce collections and notes from this area has failed to turn up any evidence of *Herrania Camargoana* in the extensive material which this early explorer gathered in the long period (1851–1856) which he spent in diligent study of the area to which the species is confined.

There has been no collection of *Herrania Camargoana* made as yet from Venezuela, but it is undoubtedly represented in the upper Río Negro drainage area of that country.

Herrania Camargoana was named in honor of Dr. Felisberto Camargo, founder and first director of the Instituto Agronômico do Norte in Belém do Pará, Brazil.

5. **Herrania Cuatrecasana** García-Barriga, Caldasia 2: 57. *t. 2.* 1941.

DISTRIBUTION: Upper reaches of the Putumayo River in Colombia.

Small tree 9 feet tall with whitish, maculate bark. Petioles terete, densely brown-stellate-tomentose. Leaves digitate, large, long-petiolate, 7-foliolate. Leaflets sessile, spreading, oblanceolate-oblong, the margins very remotely and obscurely crenate-denticulate, acuminate, basally long and gradually attenuate-decurrent, the lower leaflets about 33 cm. long, 9 cm. wide, the middle 50 cm. long, 17 cm. wide; the leaf surface papyraceous, above sparsely and minutely stellate-pubescent, the veins brown-tomentose, beneath softly stellate-pilose, the veins more prominent and hirsute above than beneath. Inflorescence fasciculate, 80–90-flowered. Flowers cauline, growing from the upper portions of the trunk, pedicellate. Pedicels slender, articulate, stellate-tomentulose, 2–3 cm. long, basally subtended by a linear or filiform, pilose, caducous bract. Buds ellipsoid or globose, 8–9 mm. in diameter. Sepals 3, equal, oblong, obtuse, dark purplish red, outwardly stellate-pilose with long hairs, inwardly with very short, reddish hairs, 15–18 mm. long, 7–11 mm. wide. Petals concave, rotund-ovate, strongly cucullate, glabrous, muricate-papillose, longitudinally striate-nerved, 10–11 mm. long, 7–8 mm. wide, with a long, filiform ligule, 130 mm. long, 1.5 mm. wide. Staminal tube 5-parted, with the stamens all bearing 4 anthers. Staminodes petaloid, purple, rhomboid-lanceolate, attenuate towards the apex, rather obtuse or acute, 25 mm. long, 8 mm. wide. Ovary shortly depressed, ovoid, densely pilose with whitish yellow hairs, 2 mm. long. Stigmas 3. Fruit ellipsoid, about 11–12 cm. long and 7–8 cm. in diameter, apically attenuate-acuminate, 10-costate, with 5 primary and 5 secondary ribs, cultriform, covered, especially along the ribs, with very minute stinging, stellate hairs, rind very thin and brittle, yellow when ripe. Seeds about 60, regular, compressed, triangular in outline, 14 mm. long, 12 mm. wide, 5 mm. thick, enveloped in a white, mucilaginous pulp, covered with a coriaceous tegument, exteriorly rugose.

Colombia. PUTUMAYO: Río Guamués, San Antonio de Guamués, alt. about 310 m., *Cuatrecasas 11168* (Type); Río Uchupayaco, alt. 300 m., *Schultes 3342*; Mocoa and vicinity, alt. 1800–2400 ft., *Schultes & Cabrera 19100*; *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *80*; Río Caquetá, Puerto Limón, *Schultes & Cabrera 18712, 18715*; Río Putumayo, Puerto Ospina and vicinity, *Schultes & Cabrera 18976*; Montclar, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *86.*

Ecuador. Río Sucumbios, 17 hrs. by motor upstream from Puerto Ospina. *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *84.*

Apparently the closest ally of *Herrania Cuatrecasana* is *H. tomentella.* This relationship is discussed under *Herrania tomentella.*

Herrania Cuatrecasana has been considered to be related to *H. Mariae* through the concept *H. Mariae* var. *putumayonis.* It differs from *H. Mariae* chiefly in having leaflets which are very much more long-attenuate-decurrent at the base, in the indument and size of the leaflets, in the length of the pedicels, in having obtuse instead of acute sepals, and in having

very characteristic and conspicuous rhomboid-lanceolate staminodes, and in the length of the petals. It is much more softly and densely pubescent than *Herrania Mariae*. It is also apparently a very much smaller and weaker plant than *H. Mariae*.

Herrania Cuatrescasana likewise resembles *H. Dugandii* in some respects. The former differs from the latter principally in having denticulate, instead of almost entire, leaf margins and in being puberulent on both surfaces of the leaflets instead of being glabrous above. Furthermore, *Herrania Cuatrecasana* has many-flowered (80–90) inflorescences, whereas *H. Dugandii* has an inflorescence composed of but twenty flowers or fewer. The pedicels of the flowers of the former species are twice as long as those of the latter, and there are important differences in the shapes and sizes of the floral parts and leaflets.

Vegetatively, *Herrania Cuatrecasana* bears some resemblance to *H. nycterodendron*; this will be discussed under that species.

The description of the fruit of *Herrania Cuatrecasana* is based upon *Schultes 3342* from the Putumayo. The leaves and dried remains of floral parts adhering to the ripening fruits as well as floral parts which were collected on the ground at the base of the tree have enabled me to determine the specimens as representing the species in question.

The specific epithet *Cuatrecasana* honors the botanist Dr. José Cuatrecasas, formerly of the Instituto de Ciéncias Naturales in Bogotá, and the Chicago Natural History Museum, now at the Smithsonian Institution.

6. **Herrania Dugandii** García-Barriga, Caldasia 2: 59, 61. *t. 3.* 1941.

DISTRIBUTION: Westernmost Amazonia, especially in the Putumayo basin of Colombia.

Small tree, 9 feet tall, sparsely branched at the apex of the trunk. Petioles terete, densely hirsute with reddish stellate hairs, 30 cm. long. Leaves digitate, long-petiolate, 7-foliolate. Leaflets sessile and spreading, the margins almost entire or near the apex slightly sinuate, obovate-oblong, acute or obtusely subacuminate, basally gradually attenuate, the lower 18 cm. long, 6 cm. wide, the middle 31 cm. long, 12 cm. wide; leaf surface firmly papyraceous or thinly coriaceous, above glabrous or very remotely strigillose, the nerves subimpressed and pubescent, beneath stellate-hirsute, roughish, the nerves reddish hirsute. Inflorescence axillary, 15–20-flowered. Flowers cauline in contracted, subumbelliform racemes, on the upper portions of the trunk, dark purple, pedicellate. Pedicels very densely brown-tomentose, articulate, 1 cm. long or shorter, basally subtended by a short linear, villous, caducous bract. Bud ovoid-oblong, 11 mm. in diameter, 18 mm. long. Calyx subcymbiform. Sepals 3, oblong, obtuse, dark purple, externally subdensely armed with stellate hairs, internally with very short rust-red hairs, up to 21 mm. long and 12 mm. wide. Petals concave, obovate, basally slightly attenuate, striate-nerved, glabrous, 11–12 mm. long, 5–6 mm. wide, apically strongly cucullate, with a long ligule. Ligule filiform, dark purple, 100 mm. long, 2 mm. wide. Staminal tube

5-parted. Staminodes narrowly lanceolate, basally and apically attenuate, apically very acute, squamulate-rugulose on both surfaces, 12–15 mm. long, 5 mm. wide. Ovary 4 mm. long, 3 mm. in diameter, densely covered with yellow hairs. Stigmas 5. Fruit unknown.

Colombia. PUTUMAYO: Río Putumayo, Puerto Porvenir, above Puerto Ospina near La Loma, alt. 230–250 m., *Cuatrecasas 10742* (Type). AMAZONAS: Trapecio Amazónico, Río Loretoyacu, alt. about 100 m., *Schultes 6038*.

Herrania Dugandii seems to be most closely allied to *H. kofanorum*, a species from the same general region. Both are rather similar in their vegetative parts, although the leaflets and certain floral parts of the latter are very much larger than those of the former. *Herrania kofanorum* further differs from *H. Dugandii* in having much more coriaceous leaflets which are more deeply and regularly undulate-sinuate; in having very strongly unequal sepals, the outer one of which is apically slit (the sepals of *Herrania Dugandii* appear at once to be much longer than *H. kofanorum* because they are much narrower in relation to their length; but, in reality, they are smaller); in having round-ovate petals which measure 9 mm. × 7 mm. (instead of obovate, basally attenuate petals measuring 11–12 mm. × 5–6 mm.); in having a more filiform ligule which measures 80–100 mm. in length × 1 mm. (instead of 100 mm. × 2 mm.); and in having much larger staminodes, which measure 22 mm. × 6 mm. (instead of about 12–15 mm. × 5 mm.). These size differences combine with slight differences in shape of floral parts to give the flowers of the two species rather dissimilar aspects. It is obvious, however, that the two are closely related. Further collections and studies, especially when the fruit of both are known, may indicate that *Herrania kofanorum* should be treated as a variety of *H. Dugandii*.

The specific epithet *Dugandii* honors Dr. Armando Dugand, outstanding botanist, and director from 1940 to 1952 of the Instituto de Ciéncias Naturales of the Universidad Nacional, Bogotá, Colombia.

7. **Herrania kanukuensis** R. E. Schultes, Caldasia 2: 11. 1943; Bot. Mus. Leafl. Harvard Univ. 13: 277. 1949; ibid. 14: *t. 33*. 1950.

Theobroma Mariae (Mart.) Decaisne ex Goudot var. *lobata* Pulle, Rec. Trav. Bot. Néerl. 9: 151. 1912.

DISTRIBUTION: Southern Venezuela, adjacent Brazil and British and Dutch Guiana.

Small tree, slender and graceful, up to 16 feet in height. Trunk with a somewhat striate, brownish-black bark. Branchlets very densely brown-tomentose. Leaves large, 5- or 6- digitate, stipulate, very long-petiolate. Stipules caducous, linear, acute, somewhat rigid and dry, very densely brown-tomentose, 15 mm. long, basally about 1.5 mm. wide. Petiole strong, up to about 53 cm. long, 6–7 mm. in diameter, very densely and softly brown-tomentose, basally rather swollen, then abruptly constricted. Leaflets sessile, unequal, strongly obovate, abruptly acuminate, basally

abruptly cuneate, almost entire, often near the apex subundulate-sinuate and often very conspicuously, though minutely, mucronate (with the prolongations of the lateral veins up to 1 mm. long), firmly papyraceous, the central leaflets 30–44 cm. long, 13–16 cm. wide, above dark green or exceedingly sparsely hirsute, aspero-strigose with long white hairs noticeable along the veins, the veins very densely and softly stellate-pilose and rust-colored, the nerves on both surfaces, but especially beneath, prominently raised. Inflorescence fasciculate. Flowers not completely known (remains of the persistent calyx showing 3 densely brown-stellate-tomentose, elliptic-lanceolate, acute sepals, 14 mm. long, 6 mm. wide; the 5 petals, concave, strongly cucullate, elongate-obovate, about 8 mm. long, 4–5 mm. wide, ligulate). Fruit long-pedunculate (peduncle rather robust, densely stellate-puberulent, up to 3 cm. long, about 2–3 mm. in diameter), ovoid, 7–8 cm. long, about 4 cm. in diameter, apically very shortly cuspidate or subrotundate, basally rounded, extremely velutinous with dense and minute stellate-puberulence, lacking stinging hairs, 10-costate, with 5 narrow and low (1 mm. wide and rarely up to 2 mm. high) blunt primary ribs and 5 secondary ribs which are similar but smaller and barely noticeable; pericarp extremely thin and apparently somewhat fragile, yellow when ripe. Seeds probably more than 60, triangular or angulate-ovate in outline, complanate, 12 × 10 × 10 mm., 4 mm. thick, in a white pulp.

Brazil. Rio Branco: lower Rio Branco, Tapanaruca, *Fróes 23003*. **British Guiana.** Northwestern slopes of Kanuku Mountains, drainage-area of Mokumoku Creek, tributary of Takutu River, alt. 150–400 m., *A. C. Smith 3541* (Type). **Dutch Guiana.** Upper River Corantijne, *Hulk 26*; River Corantijne, Kaurikreek, *Gonggrijp 2111*; *Stahel & Gonggrijp 3015*; River Coppename, *Gonggrijp 2565*; Placer L'Aiva, *Gonggrijp 4126*; River Marowijne, *Gonggrijp 4101*; near Amerikan Kondre, *Lanjouw & Lindeman 2304*; River Tapanahonie, Jaikreek, *Gonggrijp 4117*.

Herrania kanukuensis stands rather apart from the other known species of the genus. Its fruit differs strikingly from that of all other species, with the single exception of the unrelated *H. balaënsis* of Ecuador. The capsule is relatively small (measuring 9 cm. × 5 cm.) with a rounded or very shortly tipped apex (not elongate ovoid or ellipsoid with an acuminate tip, as in most species); the rind is very thin and brittle when dry (in contrast to the usual thick, leathery and fibrous condition), and the ribs are not prominent.

The few fragmentary floral parts which remained adhering to the fruit of *Smith 3541* indicate that there are also floral differences between *Herrania kanukuensis* and other species.

A duplicate type of *Herrania kanukuensis* at Kew has several leaflets which tend to be slightly irregularly dissected, suggesting a condition which approaches that of some specimens of *H. lemniscata* with abnormally developed leaflets. *Herrania kanukuensis* would appear vegetatively to be somewhat intermediate between *H. Mariae* and *H. lemniscata*,

but the indumentum on the under surface is more softly tomentose with brownish stellate hairs than in either *H. Mariae* or *H. lemniscata*.

In 1932, Uittien (in Pulle, Fl. Surin. 3: 44. 1932) reduced *Theobroma Mariae* var. *lobata* to synonymy under *T. Mariae*, identifying all of the then available material from Dutch Guiana as representing this Amazonian concept. In 1943, it appeared to me that the Surinam concept described as *Theobroma Mariae* var. *lobata* represented the plant which Schomburgk described from nearby British Guiana as *Lightia lemniscata*, and I placed it in synonymy under *Herrania lemniscata* (Schultes, Caldasia 2: 13. 1943), a species with remarkably lobate leaflets. During the war, the Utrecht material was unavailable for study. Recently, I have had an opportunity of consulting all of the Surinam specimens and am convinced that *Theobroma Mariae* var. *lobata* and *Herrania kanukuensis* represent the same concept.

From the numerous collections, for the most part from Surinam, it is now obvious that *Herrania kanukuensis* is both a widespread and, at least locally, an abundant element of the flora of Surinam, eastern British Guiana and the adjacent rim of northern Brazil.

The specific epithet *kanukuensis* is derived from the name of the Kanuku Mountains in British Guiana, where the type specimen was collected.

8. **Herrania kofanorum** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 126. *t. 28, upper fig. t. 34.* 1950.

Distribution: Upper Putumayo valley of Ecuador and Colombia.

Small tree, slender and graceful, up to 15 feet tall, usually with one trunk from each root, columnar, apically branched or unbranched, covered with an ashy black scrobiculate and scabrid bark, up to 7 cm. in diameter. Branches ferrugineous-tomentose, becoming almost glabrous, subterete and sulcate. Branchlets similar but more densely tomentose. Leaves at apex of trunk, large, digitate, very long-petiolate, 7-foliolate, stipulate. Stipules caducous, linear, acute, 2.5–3 cm. long, about 3 mm. wide, dry, outside hispidulous or strigillose, inside usually subglabrous. Petioles robust, terete but very obscurely sulcate, basally slightly dilated, subferruginous, very densely and softly tomentose, up to 30 cm. long, 6 mm. in diameter. Leaflets sessile, unequal, lanceolate-oblong, apex with a cusp about 2 cm. long, basally attenuate-decurrent, margin conspicuously and regularly undulate-sinuate; blades firmly coriaceous, mostly 17–30 cm. long, 6–11 cm. wide, above dark green, glabrous or exceedingly sparsely and very minutely strigillose-pilose with caducous white hairs, brownish-hirsute along the principal veins, beneath brownish green, very densely and softly stellate-pilose, ferruginous-tomentose along the principal veins; veins on both surfaces but especially beneath rather prominently raised. Inflorescences fasciculate, up to 20-flowered. Flowers cauline, long-pedicellate, on the lower parts of the trunk, in contracted racemes. Buds large, elongate-globose, 1.8 cm. in diameter, stellate-pilose, rather brownish red. Pedicels

strong, terete, articulate, very densely and minutely stellate-pilose, with ashy-colored hairs, mostly 9–10 mm. long, 1–1.5 mm. in diameter, at the base with small linear, acute and densely tomentose bracts, 2–4 mm. long. Calyx subcymbiform, divided almost to the base. Sepals 3, very strongly unequal, subchartaceous, entire, within minutely papillose, subglabrous and probably eventually glabrous, without sparsely stellate-strigillose, with hairs up to 1 mm. long and also with extremely minute stellate hairs, valvate in bud; the inner 2 sepals elliptic, acute, 10 mm. long, 6 mm. wide; the outer round-ovate, 15–18 mm. long, 15 mm. wide, apically rounded and often deeply (up to 2 mm.) cut, the slit extended interiorly as a furrow nearly to the base. Petals 4 or 5, round-obovate, sessile, concave, strongly cucullate, glabrous, on both surfaces (but especially on the outside) muricate-papillose or granulose, dark red, 5-nerved, striate-nerved with longitudinal purplish veins, ligulate, 9 mm. long, 7 mm. wide. Ligules filiform, pendulous, membranaceous, entirely glabrous but basally minutely granulose, about 1 mm. wide, 80–100 mm. long, at the base strongly dilated. Staminal tube 5-parted, the stamens with alternately 2 and 4 anthers and strongly flattened, short, free filaments. Staminodes conspicuously petaloid, lanceolate-elliptic, acute, basally attenuate, coarsely muricate-papillose on both surfaces, entire, 22 mm. long, 6 mm. wide. Ovary sessile, elongate-ovoid, distinctly 10-ribbed and 5-locular, yellow, very densely stellate-pilose, 2.5–3 mm. in diameter. Pistil flattened, 3 mm. long, glabrous, simple. Fruit unknown, but said to ripen yellow.

Colombia. PUTUMAYO: path between Puerto Ospina and Concepción, alt. 250 m., *Schultes 3670.* CAQUETÁ: upper Putumayo River, Caucaya, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *89.* **Ecuador.** Río San Miguel or Sucumbíos, between Río Putumayo and Quebrada Teteyé, alt. 260 m., *Schultes 3478* (Type).

Herrania kofanorum differs from its close ally *H. balaënsis* in being smaller, in having leaflets only half as large, and in having the sepals very conspicuously unequal instead of nearly alike. *Herrania kofanorum* has two inner sepals which are elliptic, 20 × 6 mm. and an outer one which is rotund-ovate, 15–16 × 16 mm., whereas *H. balaënsis* has three lanceolate-elliptic sepals which measure 14 × 6 mm. Furthermore, the outer sepal of *Herrania kofanorum* is so constructed that it is often conspicuously slit to a depth of 2 mm., and this slit is prolonged as a furrow to the base of the interior of the sepal. (When the split is not present, there is a markedly thin furrow.) Nothing similar is seen in *H. balaënsis.* Both of these species are closely related to *Herrania Dugandii.*

The specific epithet refers to the Kofán Indians who inhabit the area where the species is known to occur.

9. **Herrania laciniifolia** Goudot ex Tr. et Planch. Prodr. Fl. Novo-Granat. 209. 1862, nomen subnudum; García-Barriga, Caldasia 1: 55. *tt. 1, 4.* 1941.

Theobroma laciniifolium (Goudot ex Tr. et Planch.) De Wildeman, Pl. Trop. Grande Cult. 90. 1903.[3]

DISTRIBUTION: Middle Magdalena Valley, Colombia.

Small tree 12 to 18 feet tall with a simple, erect trunk, about 5 cm. in diameter. Leaves very large, 7-digitate, round in outline, long-petiolate, grouped towards the top of the trunk. Leaflets sessile, strongly patent, the margins deeply pinnatisect with irregular segments (similar to leaves of *Carica Papaya*), for the most triangular or lanceolate-acuminate, up to 22 cm. long and 3 cm. wide (but usually smaller), papyraceous or membranaceous, basally long-decurrent-attenuate, laciniate towards the apex, the apex itself acuminate, 38–58 cm. long, above sparsely stellate-pilose with suberect hairs along the nerves, the central and lateral veins densely red-tomentulose, beneath rather pale and rather densely and softly stellate-pubescent, with the veins as above. Petiole 25–31 cm. long, terete, striate, densely red-tomentulose, basally swollen. Flowers cauline, fasciculate, borne on upper portion of trunk, pedicellate, with the pedicel about 2 cm. long and stellate-pubescent. Sepals 4, lanceolate, rather concave, apically very acute, 17 mm. long, about 7 mm. wide, pubescent on both surfaces, externally with fewer and larger reddish stellate hairs, internally near the apex incanous, with smaller and denser hairs. Petals 5, glabrous, broadly elliptic, very concave, purplish (with yellowish veins) or "greenish white" (*Kalbreyer 2047*), apically strongly cucullate, ligulate, marginally revolute, 12 mm. long, 8 mm. wide. Ligule filiform, glabrous, red or whitish, 180 mm. long, 1 mm. wide. Staminal tube 5-parted, the stamens all 4-antheriferous. Staminodes petaloid, widely lanceolate, purple, 17 mm. long, 5 mm. wide, the margin slightly sinuous, acute or 3-dentate. Ovary globose or ovoid, 3 mm. long, densely covered with pale yellow hairs. Fruit coriaceous, oblong-ovoid, basally rounded, apically long attenuate-acuminate, the tip itself rather obtuse, 10-costate, the 5 primary ribs conspicuously raised, the 5 secondary ribs much less raised, transversely rugose, brownish red when ripe, 10.5 cm. × 5 cm. in diameter; peduncle 4 cm. long.

Colombia. [No precise locality], *Exped. Bot. Mutisii Novae-Granat. 937*; "New Granada, 4,000 ft.", *Kalbreyer 2047*. CUNDINAMARCA: Peño de Conejo, basin of Río Magdalena, *Goudot s. n.* TOLIMA: Falán, region of Calamonte, alt. 1120 m., *García-Barriga 8375*; Mariquita, alt. 547 m., Pérez-Arbeláez *10303*.

Herrania laciniifolia is apparently not an abundant element of the flora of Colombia, for it has been collected but thrice in a century, although it grows in one of the most populous parts of the nation. It is most closely allied to *Herrania lemniscata* from which it may be distinguished chiefly by having leaflets which are deeply and regularly pinnatisect (instead of very deeply and irregularly pinnatilobed). The under surface of the

[3] This combination has recently been made independently as "*Theobroma laciniifolia*" (Goud. ex Tr. et Planch.) Llano Gómez in "Cultivo del cacao" (Publ. Min. Econ. Nac., Bogota) 19. 1947.

leaflets of *Herrania laciniifolia* is very much more densely and softly stellate-pilose than in *H. lemniscata*; the leaflets are, in general, smaller; and the ligules measure 180 mm. (instead of 85 mm.) in length. The fruit of *Herrania laciniifolia* ripens red, whereas that of *H. lemniscata*, in common with all other species but one, ripens bright yellow. This other exception is *Herrania Camargoana* of the upper Río Negro basin. The fruit of *Herrania Camargoana* ripens scarlet, but this species does not appear to be closely allied to *H. laciniifolia*, and the similarity of fruit color is probably coincidental.

In the collection of Mutis plates preserved at Madrid, there are several illustrations representing *Herrania laciniifolia*. Drawn by Matíz, these are all in black and white, not in color. One plate has a leaf with a complete leaflet and a length of stem with several flowers and buds; another plate has analytical drawings of the flowers and fruits; a third has analyses only of the floral parts.

The Mutis specimen in Madrid (cited above) is sterile, but it was undoubtedly taken from the tree from which the plate was made. In view of the scarcity of collections of *Herrania laciniifolia*, it is unfortunate that a definite locality for the Mutis collection is not available. Both the specimen and the plates agree perfectly with the type and the later material of this remarkably distinct species.

10. **Herrania lemniscata** (Schomb.) R. E. Schultes, Caldasia 2: 13. 1943; Pittier et al. Cat. Fl. Venez. 2: 134, 139. 1947; R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 13: 281. *t. 30*. 1949.

Lightia lemniscata Schomb. Rep. Assoc. Advancem. Sci. 13: 71. 1844. Nomen subnudum.

DISTRIBUTION: British and Dutch Guiana and the Orinoco basin of eastern Venezuela, extending into northeastern Colombia.

Small tree, with a simple, round, slender trunk up to 30 feet tall, with leaves grouped at the tip of the trunk. Branches apparently tomentose, becoming subglabrous. Leaves very large, 7-digitate, very long-petiolate, stipulate. Stipules caducous, minutely subulate, extremely densely and softly ferruginous-tomentose, about 2 cm. long, basally 2 mm. wide. Petioles robust, terete, sulcate, apically widely complanate-flabelliform, very densely and softly rusty tomentose, slightly swollen then immediately strongly constricted, up to 45 cm. long, 8–10 mm. in diameter. Leaflets sessile, unequal, the central one up to 80 cm. long, 40 cm. wide, acuminate, basally long-decurrent-attenuate, the margin very profoundly pinnatilobate with (usually) 4 irregular, usually triangular or broadly lanceolate-acuminate segments, in the longest part of leaflet up to 18 cm. long, 9–10 cm. wide, papyraceous or membranaceous, above dark green, subglabrous or beset with very remote stellate hairs, densely ferruginous-strigillose along the nerves, beneath pale green, densely and softly stellate-pilose, the nerves densely ferruginous-tomentose, the veins prominent on both surfaces. Inflorescence fasciculate, bearing probably up to 30 or 40 (but

usually about 20) flowers. Flowers borne in contracted racemes on the lower portion of the trunk, dark crimson-purple, pedicellate. Pedicels strong, terete, minutely and densely stellate-tomentellose, articulate, 7–8 mm. long, basally subtended by a short, linear, tomentose bract, 1 mm. long. Buds globose, 9–10 mm. in diameter, very densely and minutely stellate-tomentellose and stellate-pilose. Calyx divided almost to the base, subcymbiform. Sepals 3, reflexed, almost equal, thick, internally very densely puberulent, externally very densely stellate-tomentose and stellate-pilose (2 distinct types of hairs), with an entire and strongly inflexed margin, brownish red; the two larger sepals ovate, subobtuse, 12–13 mm. long, 7 mm. wide; the smaller one lanceolate-elliptic, apically subobtuse, 13–15 mm. long, 5–8 mm. wide. Petals 5, sessile, elongate-obovate, concave, strongly cucullate, entire, dark blood-red (sometimes possibly yellowish) with 5 prominent black or purplish nerves, 6–7 mm. long, 4 mm. wide, glabrous, on both surfaces but densely muricate-papillose externally, thick, ligulate. Ligules hanging, membranaceous, filiform, glabrous, without nerves, basally 1–1.5 mm. wide, about 85 mm. long, blood-red, sometimes becoming yellowish. Staminal tube 5-parted with stamens alternately 2- and 4-antheriferous, filaments short, free and simple. Staminodes conspicuous, petaloid, dark blood-red, sometimes apically yellowish, elliptic, slightly and obscurely undulate, acuminate, 10–12 mm. long, 4–5 mm. wide, glabrous, densely muricate-granulose on both surfaces. Ovary sessile, ovoid-globose, 4.5–5 mm. long, 2.5 mm. in diameter, distantly 10-costate with 5 primary and 5 secondary ribs, yellow, very densely hispid-pilose. Style terete, glabrous, simple, with an obscurely 5-parted stigma. Fruit long pedunculate (with a strong, glabrous or glabrescent peduncle up to 4.5 cm. long and 3 mm. in diameter) perfectly ovoid, 7 cm. long, 4 cm. in diameter, apically very shortly and abruptly cuspidate, basally almost rounded, densely and minutely stellate-puberulent, apparently lacking stinging hairs, 10-costate with 5 narrow, comparatively low, subcultriform primary ribs which are 2 to 4 mm. high and 1–2 mm. thick (in the dried specimen) and 5 similar but smaller ribs, the very thin pericarp strongly reticulate-costate between the longitudinal ribs, probably yellow when ripe. Seeds apparently more than 60, triangular or angular-ovate in outline, flattened, 12 × 11 × 11 mm., above 4 mm. thick, buried in a white pulp.

British Guiana. Banks of Barima River. *Schomburgk s. n.* (Type); [no precise locality], *im Thurn s. n.* (Type of fruit); Essequibo River, White Creek, Groete Ck., *Forest Dept. Brit. Guian. Field No. F1763, Research No. 4500.* **Colombia.** SANTANDER: 15 km. east of Puerto Berrio, alt. about 250 m., *Scolnick, Araque & Barkley 195001.* **Venezuela.** Near mouth of Orinoco River, *Rusby & Squires 252*; Pakaraima Mountains, *Myers 3371.* BOLÍVAR: Salto de Pará, Medio Caura, alt. 120 m., *L. Williams 11339*; lower part of Quebrada O-paru-mo, tributary of Río Pacairao, below Santa Teresita de Kavanayen, alt. 915–1065 m., *Steyermark 60558.*

Herrania lemniscata is undoubtedly one of the most strikingly distinct species of the genus. It can be distinguished at once by its very large and

broad leaves with pinnatilobed leaflets. It is, apparently, most closely related to *H. laciniifolia* of central Colombia, but its leaflets are much more coarsely incised, with fewer and wider lobes. Florally, *H. lemniscata* does not seem to be very distantly allied to *H. Mariae* and *H. kanukuensis*.

It would appear that the Guianan *Herrania lemniscata* occupies a somewhat intermediate position between the Colombian *H. laciniifolia* on the one hand and the Amazonian *H. Camargoana* on the other. This relationship has been discussed under the latter species.

The name *Lightia lemniscata* was published by Schomburgk in 1844 without an adequate description and without the citation of specimens. It must be considered a *nomen subnudum*. Several years later, Schomburgk (Linnaea 20: 756. 1847) reduced the name to synonymy under *Herrania Mariae*, and, wishing to perpetuate a generic name honoring Governor Light of British Guiana, he transferred the name *Lightia* to a new genus in another family.

In 1848, he (Schomburgk, Fauna und Flora von British-Guiana. 993. 1848) listed under *Herrania Mariae* specimen(s) which he had collected in British Guiana along the River Barima and its affluents. It is probable, then, that this represents the area from which the type material of *Lightia lemniscata* came.

Fortunately, I have had an opportunity to study a beautiful collection (*Archer 2514*) from this same region. I have considered it as a topotype, although it must be remembered that Schomburgk's mention of the "River Barima and its affluents" circumscribed a rather extensive area.

All of the material of *Herrania* from British Guiana and northeastern Venezuela which I have seen is (with exception of collections from near the Brazilian border) referable to one species. This species is distinct from others of Middle and South America. I am inclined to believe that these specimens are referable to the concept which Schomburgk called *Lightia lemniscata*.

In the New York Botanical Garden there is a specimen collected in the easternmost part of Venezuela near the mouth of the Río Orinoco in 1896 (*Rusby & Squires 252*). On the label of this specimen, a handwritten notation states: " = *coll. by Schomburgk in Brit. Gui.*" On the basis of this annotation and the near homogeneity of the Guianan collections, I validated Schomburgk's *nomen subnudum* and transferred it to the genus *Herrania* in 1943.

When I validated the Schomburgk concept, making the new combination *Herrania lemniscata*, European collections were unavailable for study. Recently, additional and extensive material which I have seen in England indicates that *Herrania lemniscata* is indeed a very distinct species. Schomburgk's original water-colors, made in the field, are preserved at the British Museum (Natural History). Included in the collection is an excellent painting of this concept (as *Lightia lemniscata*) which depicts with unusual accuracy the habit of the small tree. There is, likewise, what appears to be a Schomburgk water-color attached to one of the herbarium sheets at Kew.

The collection *Myers 3371* consists only of flowers. It is referred with some reservation to *Herrania lemniscata*. The collection *L. Williams 11339* has been reported in the literature (L. Williams, Exploraciones botánicas en la Guayana venezolana. 309. 1942) as *Herrania Mariae*.

By using the specific epithet *lemniscata*, Schomburgk intended to call attention to the very long ribbon-like ligules which adorn the flower.

11. **Herrania Mariae** (Mart.) Decaisne ex Goudot, Ann. Sci. Nat. III. **2**: 233. 1844.

Abroma Mariae Mart. Denkschr. Regensb. Bot. Gesell. **3**: 297. *tt. 6, 9.* 1841.
Theobroma Mariae (Mart.) Schum. ex Mart. Fl. Brasil. **12**(3): 71. *t. 15.* 1886; Ducke, Rodriguesia **4**: 273. *t. 5, fig. 2. tt. 6, 7.* 1940.

Distribution: General in the Amazon basin, with the exception of the northern and northwestern sectors.

Small or large tree, up to 30 (doubtfully up to 60) feet tall; trunks (often 5 or 6 from a root) erect, columnar, 7–30 cm. in diameter, with brownish-black or black, rimose or scrobiculate bark. Branches sometimes closely crowded, forming a subglobose crown, in which the lower branches are subhorizontally spreading, rather flexuous, sometimes few and wide-patent; ferruginous-tomentose but becoming subglabrous, subterete, sulcate. Branchlets similar, spreading. Leaves large, digitate, long-petiolate, 6–9 (usually 7-) -foliolate, stipulate. Stipules caducous, linear, acute, 2.5–4 cm. long, about 3 mm. wide, dry, tomentose. Petioles strong, terete, subsulcate, basally somewhat swollen, 30–50 cm. long, 7 mm. in diameter, subferruginous, very densely and softly tomentose with erect, brown, stellate hairs. Leaflets thin-membranaceous to thin-papyraceous, sessile, unequal, usually strongly rhomboid-ovate, apically acuminate (acumen about 2 cm. long), basally attenuate-decurrent, entire or very slightly subundulate towards the apex and conspicuously armed with small, spine-like, hirsute, mucronulate prolongations of the veins up to 1 mm. long; the leaf surfaces usually 27–54 cm. long; 7–19 cm. wide, above dark green, very sparsely and minutely hirsute (or, in rare specimens, subglabrous) with white hairs (very rarely with brownish stellate hairs), more densely hirsute along the principal veins and along the margin, beneath pale green, subasperous or soft with minute stellate-sericeous hairs, ferruginous-tomentose along the principal veins; the veins prominent on both surfaces, but conspicuously elevated beneath. Inflorescences fasciculate, usually few-flowered (with about 10–15 flowers) but frequently many-flowered (80–90). Flower buds subglobose, large, 17 mm. in diameter, densely stellate-hispid. Flowers cauline, long-pedicelled, growing from the middle and lower portions of the trunk in contracted racemes. Pedicels densely fulvo-tomentose, hispidulous with minute, appressed strigillose hairs and also sparsely setose, articulate, 1.5–5 cm (mostly 3.5–5) long, basally subtended with a short linear, acute, densely tomentose bract 3 mm. long. Calyx subcymbiform, divided nearly to the base. Sepals 3–5, strongly unequal, entire, externally densely stellate-strigose, internally glabrous,

or very minutely pilose, thick-membranaceous, brown, valvate in bud later reflexed, longitudinally striate; the interior broadly elliptic-oblong, apically subacute, with coarse hairs frequently up to 1 mm. long, 12–15 mm. long, 6–10 mm. wide; the exterior very broadly rotund or broadly ovate, apically abruptly and obscurely acuminate, with coarse hairs 1 mm. long, 11–13 mm. long, 11–12 mm. wide. Petals 4 or 5, basally sessile, concave, rotund-obovate, apically very strongly cucullate, 7–9 mm. long, 6–8 mm. wide, glabrous, muricate-papillose on both sides, 5-nerved, pale purplish red with black or purple veins, apically ligulate. Ligules filiform, pendulous, membranaceous, pale yellow or white, with purple venation, minutely granulose in all parts but especially so at the base, basally up to 4 mm. and apically hardly 1 mm. wide, 75–100 mm. long (very rarely less), apically slightly coiled. Staminal tube 5-parted, stamens alternately 2- and 4-antheriferous, filaments short and free, anthers yellow. Staminodia conspicuous, petaloid, reflexed, red, lanceolate or lanceolate-elliptic, apically obtuse and usually indentate mucronate or serrate, somewhat sinuate-undulate, glabrous, muricate-granulose on both sides, up to 20 mm. long, 6–7 mm. wide. Ovary sessile, elongate-subglobose, pentagonal (distinctly 10-costate and 5-locular), densely stellate-pilose, rose-colored or yellow-white. Style short, subcylindric-pentagonal, reddish. Stigmas 5, filiform, rose-colored. Fruit baccate, elliptic-ovoid, apically acuminate, long-peduncled (peduncle up to 2.5 cm. long), conspicuously 10-costate; the 5 primary ribs large, protruding, acute-scutelliform, about 8 mm. tall, 5 secondary ribs similar but smaller, about 4 mm. tall, conspicuously fibrous-striate transversely between the ribs, very densely stellate-hispid with stinging hairs along the ribs, up to 10–12 cm. long, 6–7 cm. in diameter, pericarp thick, subsucculent (not conspicuously fibrous), yellow when ripe. Seeds 30–40 (possibly –60), obtusely rhomboid, flattened, with a subcoriaceous testa, about 10 cm. long, 9 mm. wide and 4 mm. thick, in a white, acidulous pulp.

Brazil. AMAZONAS: Rio Solimões, *von Martius s. n.* (Type); Paleta, Teffé, *Krukoff's 4th Exped. Brazilian Amazon 4523*; Fonte Bôa, *Fróes 20630*; Rio Jurua, Marary, *Ule 5031*; Rio Amazonas, Taperinha, near Santarém, *Ginzberger 804*; Rio Madeira, Humayta, near Tres Casas, *Krukoff's 5th Exped. Brazilian Amazon 6085*; Riosinho, Juruema, *Fróes 21041*. PARÁ: Belém, *Ducke 595*; Museu Goeldi, *Murça Pires & Black 740*; Utinga, *Schultes 8072*; Belterra, *Black 47–1916*. **Colombia.** AMAZONAS: Trapécio Amazónico, interior regions of trapecio between Amazon and Putumayo watersheds, alt. about 100 m., *Schultes 6759*; mouth of Río Atacuari, *Black & Schultes 46–223*. **Peru.** MADRE DE DIOS: near Iberia, *Schultes 6461*.

Due primarily to the detailed drawing of *Herrania Mariae* which was published in *Flora Brasiliensis* and to the general availability and reliability of this work, botanists have had a tendency to consider as representing this species collections from a wide area but which actually belong to very diverse concepts. Almost all collections in our herbaria have been referred to *Herrania Mariae*. Indeed, very recently, Ducke has stated that *Theo-*

broma Mariae is "the only species in the Brazilian Amazonia representing the subgenus (or section) *Herrania* . . . ," that this "species is found throughout the hylea (including the Guianas) . . . ," and that "it is probable that, in addition to *atrorubra*, still other species of the subgenus *Herrania*, described from northern and northwestern South America, will in the future be reduced to synonymy under *Theobroma Mariae*" (Rodriguesia 4: 273. 1940).

Herrania Mariae is probably the tallest species in the genus and, unlike almost all other species (except *H. pulcherrima*), it often has many trunks growing from one root. Martius described the plant as being 20–30 feet in height, and the drawing which was published with the original description shows an extremely robust and corpulent tree with a basal diameter of some 15–30 cm. and with a very heavy, round and full crown. My field work with *Herrania* leads me to believe that this drawing, herein reproduced for historical reasons, is erroneous and greatly exaggerates the size of the trunk and crown. Ducke commented similarly on this illustration when he wrote (loc. cit.), "In Martius' drawing, reproduced in 'Flora Brasiliensis,' *Th. Mariae* appears as a much-branched tree which does not in any way correspond with the real habit of our plant . . . ." The few collections of this widespread species which are at hand at the present time exhibit some variation, but an abundance of comparative material is lacking for determining with precision the character and extent of the variation. I am certain that when more abundant collections and field observations have been made, it will be necessary to recognize several definite geographical variants. An example of our inability to treat with complete certainty some collections is seen in *Krukoff 6085* which may possibly be an hybrid between *Herrania Mariae* and *H. nitida*. *Schultes 6238* and *6461*, unfortunately sterile, represent perhaps one of the extremes exhibited by the available material of *Herrania Mariae*. They are the southernmost collections of the genus, occurring on high land which never floods (in contrast to the flood-land habitat of the banks of the Amazon), and appear to have on the under surface of the leaflets a much denser and softer indumentum which tends to be rather greyish in life.

In the herbarium at Munich, there are seven very ample specimens of Martius' type collection. A study of this material has enabled me to evaluate the concept more critically. The type material has extremely membranaceous to very thinly papyraceous leaflets which have a rather softly asperous indumentum on the lower surface and a sparse asperous pilosity on the upper. The leaflets are strongly rhomboid-obovate, a shape which is peculiar to *Herrania Mariae*. The petiole, shorter and less robust than in most species, is densely tomentose, and the inflorescence is many-flowered.

Herrania Mariae is related to *H. Cuatrecasana*, *H. nitida* and *H. pulcherrima*. All four species have a similar type of fruit with very large and protruding cultriform ribs which are unequal and with strong transverse wrinkles between the ribs and more or less at right angles to them.

Herrania Mariae resembles *H. Cuatrecasana* very closely in some char-

acters, and I once suspected that the latter might well be considered a variety of the former. Further field work and additional collections of *Herrania Cuatrecasana*, however, and the discovery of *H. Mariae* var. *putumayonis* give us reason to maintain the two concepts as completely distinct. The most obvious difference between the two species is the shape of the leaflets: very long oblanceolate-oblong and very long and gradually attenuate towards the base in *Herrania Cuatrecasana* and rhomboid-obovate and more abruptly attenuate towards the base in *H. Mariae*; the leaflets of the former are also usually very much longer than those of the latter species, and the petiole is much longer, stouter and more softly ferruginous-tomentose. *Herrania Mariae* has lanceolate or lanceolate-elliptic, somewhat sinuate-undulate and apically often serrate or indentate-mucronulate staminodes which are, for the most part, 20 mm. long and 6–7 mm. wide, whereas *H. Cuatrecasana* has definitely rhomboid-lanceolate, entire and apically non-serrate staminodes which measure 25 mm. long and 8 mm. wide. The ligule of the former species usually measures from 75 to 100 mm. in length, of the latter, 130 mm.

The differences which set *Herrania Mariae* apart from *H. nitida* are very evident. The latter is separated at once from the former by its complete lack of indumentum on the leaflets (or, when slightly tomentulose underneath, by the sparsity and asperous nature of the hairs); by its leaflets which are usually lanceolate-elliptic, more firmly chartaceous and most often entire; and by a number of floral characters.

Herrania pulcherrima is most easily separated from *H. Mariae* by the enormous size of its leaflets (up to 60 cm. long) which are oblong, for the most part about half as wide or wider, with the secondary and tertiary veins extraordinarily conspicuous and raised beneath, giving the upper surface, in most specimens, a verrucose appearance; by the unusually long and strong petioles; and by the larger flowers which are dark red in all parts, excepting the ligules which in some specimens are cross-banded scarlet and whitish. Both of these species have a characteristically trifid staminode.

With the specific epithet of *Herrania Mariae* Martius honored Maria, Queen of Saxony, whose father, King Maximilian Joseph of Bavaria, patronized Martius' extensive botanical explorations in South America.

Van Hall (Cacao. ed. 2. 74. 1932) states that seeds of this species are occasionally found as an adulterant in "Pará cacao", but it is not certain that his identification can be taken as reliable: his confusion of *Herrania Mariae* with another species is obvious from the statement that "it is very common in the forests of Surinam near Paramaribo and also deep into the interior" (loc. cit.).

11a. **Herrania Mariae** (Mart.) Decaisne ex Goudot var. **putumayonis** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 129. *i. 30, upper fig.* 1950.

DISTRIBUTION: Western part of the Amazon Valley, especially in the Putumayo River basin.

Small tree up to 12 or 14 feet tall, differing from *Herrania Mariae* chiefly in having much larger (up to 52 cm. long, 18 cm. wide), lanceolate-elliptic (not conspicuously rhomboid) leaflets; stronger and longer petioles; larger flowers up to 17 mm. in diameter, with the buds globose, and shorter ligules up to 70 mm. long, but usually somewhat less.

Brazil. AMAZONAS: Rio Jurua, Lago Cerrado, *Traill 65*. **Peru.** LORETO: Río Putumayo, between Río Igaraparana and Río Yaguas, alt. 100–150 m., *Schultes 4010* (Type).

Additional material may indicate that this concept is deserving of specific rank. At the present time, however, it would seem advisable to treat it as representing a variety of *Herrania Mariae*. The fruit of *Schultes 4010* is hardly distinguishable from that of typical *Herrania Mariae*. The flowers have several differentiating characters, the most conspicuous of which is the shorter ligule. Vegetatively, the collection is extremely similar to *Herrania nycterodendron* (with the type plant of which it was growing) and differs markedly from *H. Mariae* chiefly in the departure from the typical rhomboid form of the leaflets and in their unusually large size. The type plant of *Herrania Mariae* var. *putumayonis* consisted of four or five trunks in a clump, whereas *H. Mariae* is a treelet with a single trunk, although the condition of several trunks from one root is not uncommon in *H. Mariae*.

In the Paris herbarium there is a specimen, the collector and date of which we are ignorant, referable with reservation to *Herrania Mariae* var. *putumayonis*. It was collected at the upper Amazon town which is now called Teffé: "fluv. Amaz. Ega. *2660. Abroma* n. sp. Arbor debilis." The specimen is sterile, but it was thus early recognized as a distinct concept.

Herrania Mariae var. *putumayonis* may represent a western variant of the species which is most abundant in the eastern half of the Amazon basin. The varietal epithet refers to the Putumayo River.

12. **Herrania nitida** (Poepp.) R. E. Schultes, Caldasia 2: 16. *t. pag. 17.* 1943.

Abroma nitida Poepp. in Poepp. & Endl. Nov. Gen. ac Sp. Pl. **3**: 73. 1845.
Brotobroma aspera Karst. & Tr. ex Tr. Nuev. jén. y esp. pl. fl. Neo-Granat. 12. 1854.
Herrania aspera (Karst. & Tr. ex Tr.) Karst. Linnaea **28**: 447. 1857.
Theobroma nitidum (Poepp.) Schum. ex Mart. Fl. Brasil. **12**(3): 72. 1886. Non *T. nitida* Bernoulli, Neue Denkschr. all. Schweiz. Gesell. gesam. Naturw. **24**(3): 15. *t. 17, fig. 3.* 1871.
Herrania atrorubens Hub. Bull. Soc. Genève II. **6**: 187. 1914.
Theobroma aspera (Karst. & Tr. ex Tr.) Van Hall,[4] Cacao. ed. 2. 49. 1932.

[4] This combination was made, but imperfectly so, by van Hall who, in a key, refers to "*T. aspera* (Karsten) Schumann". He refers to Schumann's account in Martius' Flora Brasiliensis where *aspera* is not mentioned under *Theobroma*, *Herrania* or *Brotobroma*; and there is no evidence that Schumann ever made the combination.

Herrania nitida (Poepp.) R. E. Schultes var. *aspera* (Karst. & Tr. ex Tr.) R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 130. 1950, *pro parte*.

DISTRIBUTION: Widespread in the western half of the Amazon Valley and the Orinoco basin in Colombia.

Small tree, rather weak, graceful, probably up to 12 feet tall, with dark brown, roughened bark; the trunk usually less than 7 cm. in diameter at the base. Branches sparsely and minutely tomentose, becoming glabrous. Petioles subcomplanate, conspicuously striate-sulcate, ferruginous, very minutely closely appressed stellate-tomentulose, basally somewhat swollen, up to 40 cm. long, 5 mm. in diameter. Leaves grouped at the apex of the trunk, 7–9-digitate, long-petiolate, stipulate. Petiole usually slender, asperous, very minutely ferruginous-tomentulose, sometimes becoming subglabrous, terete but very deeply sulcate, up to about 40 cm. long, basally 4–5 mm. in diameter. Stipules linear, up to 2.5 cm. long, 1 mm. wide, usually brown stellate-setulose. Leaflets sessile or nearly so, unequal, lanceolate-oblong, acuminate, basally very long attenuate-decurrent, marginally entire, rigid-chartaceous to subcoriaceous, light green, shiny, glabrous above, glabrous or rarely with very sparse and deciduous minute stellate hairs remotely placed along the nerves beneath; the central leaflets 25–45 cm. long, 7–14 cm. wide; the lateral leaflets much smaller and often asymmetrical. Inflorescence fasciculate; often very numerous on the basal portion of the trunk, up to 30–40-flowered. Flowers cauline, pedicellate. Pedicels articulate, densely appressed. tomentulose with occasional strigose setae, 5 mm. long, less than 1 mm. wide. Calyx subcymbiform. Sepals 3, yellow-red, externally very coarsely stellate-setose, internally glabrous; outer sepal rounded-ovate, or triangular-ovate, up to 14 mm. long 10 mm. wide (but usually smaller); inner sepals elliptic, acute, up to 17 mm. long (but usually shorter) 6 mm. wide. Petals 5, broadly obovate, rotund, 4–5 mm. long, 4–5 mm. wide at the top, strongly cucullate, fleshy membranaceous, very densely muricate-papillose on both sides but especially without, glabrous, longitudinally marked with 5 or 6 dark red veins, yellowish-rose or rose-white, ligulate. Ligules linear, hanging, basally slightly contracted, apically slightly coiled, pink or scarlet, up to 80 mm. long, membranaceous, glabrous, longitudinally marked with five purple nerves. Staminal tube 5-parted, alternately 2- and 4-antheriferous with simple, flattened, free filaments. Staminodes conspicuous, petaloid, glabrous, muricate-granulose, elliptic, acute, marginally slightly undulating, dark blood-red without, yellowish-red within, 9 mm. long, 5 mm. wide. Ovary 5-locular, subcylindric, densely and very minutely stellate-pilose, yellow, about 1.8 mm. long, 1 mm. in diameter. Style strongly flattened, 3 mm. long, with a simple stigma. Fruit baccate, ovoid, acuminate, 11 cm. long, 5 cm. in diameter, dull, rich green, 10-costate, the 5 primary ribs thin, cultriform, basally up to 2.5–3 mm. and apically 1.5 mm. thick, 8–9 mm. high, the 5 secondaries similar but smaller, minutely and very densely beset with stinging hairs along the ribs; pericarp between the ribs usually smooth and not fibrous-rugose, very thin, sometimes with a few stinging hairs but becoming glabrescent. Peduncle short and strong, usually under

14 mm. long, 2.5 mm. in diameter. Seeds 30–40 or more, flattened, roughly triangular in outline, 9 mm. × 8 mm. × 5 mm., in a white pulp.

Brazil. AMAZONAS(?): *Glaziou 9635*. AMAZONAS: Rio Purus, varzea at Sobral, *Traill 64*; Rio Solimões, Santo Antonio do Içá, *Ducke 7618*; Benjamin Constant, *Fróes 20919*; Amaturá, *Ducke s. n.*

Colombia. AMAZONAS: Río Amazonas, La Victoria, *L. Williams 2816, 2843*; Leticia, alt. about 100 m., *Schultes 6000, 6016, 6141, 6142, 6143, 6144, 6145, 6146, 6147, 6149, 6192a*; Río Loretoyacu, *Schultes 6304, 6045, 6058, 6118, 6124, 6640, 6878, 8129, Schultes & Black 8286, 8377*; Río Apaporis, between Río Pacoa and Río Kananarí, region around Soratama, alt. 250 m., *Schultes & Cabrera 13628, 13630, 13632, 14880, 14882*; *Schultes & García-Barriga 14016*; Río Caquetá, La Pedrera, *Schultes 5876*; *Anglo-Colombian Cacao Collecting Expedition* (*Baker & Cope*) *17, 19, 22, 24*. CAQUETÁ: Río Orteguaza, Tres Esquinas, *Schultes 3698*; upper Río Putumayo, Montclar, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *85*; Caucaya, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *87, 88*; Río Caucaya, Laguna Primavera, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *92*; Río Caguan, Arbolitos, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *100*; Camp Three, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *112*; Cartagena, *Anglo-Colomb. Cacao Coll. Expedition* (*Cope & Holliday*) *106*; Río Caqueta, Camp Five, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *120*. PUTUMAYO: Río Putumayo, Puerto Ospina, alt. about 280 m., *Schultes 3405*, *Schultes & Cabrera 18933*; Río Caucaya, *Schultes 3730*. VAUPÉS: upper Apaporis basin, path between Río Itilla and Río Macaya, alt. 300 m., *Schultes 5351*; Río Macaya, Cachivera del Diablo, alt. 350 m., *Schultes 5491*; near confluence of Río Ajaju and Río Macaya, Puerto Hevea, alt. 350 m., *Schultes 5529*; middle Apaporis basin, Río Kananarí, Buenos Aires, alt. about 250 m., *Schultes 5685*; Río Apaporis, Jinogoje, *Anglo-Colomb. Cacao Coll. Exped.* (*Baker & Cope*) *10*; Río Vaupés, Puerto Naré, *Schultes 5359*; near Miraflores, *Schultes 5715*; La Jirisa, *Schultes 5755*; near mouth of Río Kubiyú, *Schultes & Cabrera 14537*; Circasia, alt. 800 ft., *Schultes & Cabrera 19665*; between Mitú and Javareté, Igarapé, Murutinga, near Tipiaca, *Schultes & Cabrera 19284*; Río Kuduyarí, Cerro Yapobodá, *Schultes & Cabrera 14343*; near Irabasú, *Schultes, Baker & Cabrera 18439*; lower course of Río Kuduyarí, alt. 700–800 ft., near Yararacá, *Schultes, Baker & Cabrera 18553*; Río Paca, Wacaricuara, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *55c*; Río Inirida, Caño Caribe, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *67*; Río Papunawa, near junction with Río Inirida, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *76*. META: Villavicencio, alt. 400 m., *Triana s. n.*, *Killip 34247*; Llanos de San Martín, near Villavicencio, alt. 400 m., *Triana 5333*; Cordillera La Macarena, path between Río Guejar and Caño Guapayita, Cano Yerly, *Idrobo & Schultes 768*, *Schultes 11627*; savannahs near San Juan de Arama, Río Guejar, near landing strip "Los Micos", alt. about 500 m., *Idrobo & Schultes 1325*.

Ecuador. Río Pastaza, near Andrés, *Spruce 4969*.

Peru. [No precise locality], "*Herb. Pavon*". SAN MARTIN: Río Tocache, *Poeppig 1979* (Type). LORETO: Río Marañón, near Pongo de Manseriche, *Tessmann 4024*; Iquitos, alt. about 100 m., *Killip & Smith 27431*, *Murça Pires & Black 873*; lower course of Río Huallaga, between Yurimaguas and Balsopuerto, alt. 135–150 m., *Killip & Smith 28234*; Río Amazonas, Caballo Cocha, *L. Williams 2332*; upper course of Río Itaya, San Antonio, alt. 145 m., *L. Williams 3345*; Paraíso, alt. 145 m., *L. Williams 3364*.

Herrania nitida is the most widespread species in the genus, extending from the eastern slopes of the Andes in Colombia, Ecuador and Peru throughout the entire Amazon basin, being especially concentrated in the western half. As should be expected, therefore, there is evident considerable variation within the concept. It is undoubtedly the most variable species of *Herrania*, and further collections and studies will probably indicate that some of the variations are deserving of taxonomic recognition. To date, however, I have been able to separate out only one variant which is recognized now as a *forma*.

One can think of *Herrania nitida* as a kind of evolutionary center. It is in itself most distinct from all other species, but in certain respects some of its variants approach the variants of other species. Its foliage resembles that of *Herrania albiflora* and *H. purpurea* to a remarkable degree, but there are no floral or fruiting characters which point to even a remote relationship. *Herrania nitida* has often been confused with *H. Mariae*, usually because, in spite of its specific epithet, it has variants with leaflets softly tomentose (even though always sparsely so), especially in the central and eastern parts of the Amazon Valley. Indeed, one collection (*Krukoff 6085*) is so intermediate between these species that I have indicated (under *Herrania Mariae*) that it may possibly represent a hybrid of the two. Very significant floral characters (coloration, size and shape of the staminodes, form of the style, and placement of the anthers) serve easily to set the two apart; and the peculiar rhomboid-obovate leaflets of *Herrania Mariae* contrast strikingly with the lanceolate-oblong leaflets of *H. nitida*. We can see from the similarity in the fruit, however, that these two species are more closely allied than one would suspect from a study of the floral and vegetative parts.

The flower of *Herrania nitida* is one of the smallest and most delicate in the genus. Usually there is a general tendency in the staminodes and even in the petals for a yellowish tinge, with nerves which are the more conspicuous in these parts because of their dark purplish color against the yellow. The ligules are almost always yellowish or white in the upper half, but there are variants which have very dark scarlet ligules. The leaflets of *H. nitida* are generally drooping, a characteristic which I have not seen commonly in other species.

Herrania nitida prefers well-drained sloping soil, usually of a semi-lateritic consistency, and is rarely found where the annual flood of the rivers remains long enough and becomes deep enough to produce a drowning effect. It is most often rather abundant in the areas where it occurs.

In 1950, when I reduced *Herrania aspera* to a varietal status under *H. nitida*, I pointed out that there has been confusion in the presentation of this concept since 1857, when Karsten stated that it was found "in vallis Orenocensis marginibus ad pedem Andium bogotensium meridensiumque . . . et littora fluminis Magdalenae". It was difficult to accept the occurrence of the same species on both sides of the great Andean cordillera, and Karsten's assertion may have been based on the study of a sterile specimen of *Herrania albiflora* Goudot. Later, Triana and Planchon (Prodr. Novo-

Granat. 209. 1862) erroneously reduced *Herrania aspera* to synonymy under *H. pulcherrima* Goudot. A further confusion resulted with my treatment of *Herrania aspera* as a variety of *H. nitida*.

A study of the fruit and flowers of the Macarena material indicates that this plant, which represents a hitherto undescribed concept and which has, in part, been referred in the past to *H. aspera*, bears little relationship to *Herrania pulcherrima* and none to *H. nitida*. The confusion which has resulted in the past appears to be directly a result of two factors: incomplete material and Karsten's failure to cite a definite specimen which we could take as a type. The presumed type of *Herrania aspera* has been taken as *Triana 5333* from the llanos of Villavicencio. In view of the material now available and of field studies in the Macarena not far from the type locality of *Herrania aspera*, I am now reducing *H. aspera* to synonymy under *H. nitida* and am describing *H. tomentella* to accommodate the soft-pilose, large-leaved plant which is common in the western part of the Llanos and in the Macarena.

Herrania atrorubens is also herewith reduced to synonymy under *H. nitida*. When Huber described *Herrania atrorubens*, he cited his collection *7935* from the Alto Amazonas of Brazil as the type and only material of the concept. He stated that it differed from *Herrania Mariae* in being smaller and in having dark red flowers. In 1944, in treating this binomial (Caldasia 2: 329. 1944), I wrote, "I have been unable to examine the type of this concept. Without typical material, I have found it impossible to estimate its validity as a species, but it would seem that the colour character alone would hardly suffice for the creation of a new specific concept."

Now, having completed an extensive study of the classical material of the genus, I have been unable to locate the type of *Herrania atrorubens*. One would expect it to be preserved in the Museu Goeldi in Belém do Pará or in the Herbier Boissier in Geneva, but a search in these two institutions, as well as in other principal Brazilian and European herbaria has not uncovered Huber's material.

In the light of the experience gained during the study of a wide range of material, it would seem from an evaluation of the meager characters given by Huber and from the geographical data given for the type collection that *Herrania atrorubens* may be reduced safely to synonymy under *H. nitida*.

12a. **Herrania nitida** (Poepp.) R. E. Schultes f. **sphenophylla** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 131. 1950.

Herrania nitida (Poepp.) R. E. Schultes var. *sphenophylla* R. E. Schultes, Caldasia **2**: 20. 1943.

?Theobroma Mariae (Mart.) K. Schum. f. *minor* Diels, Notizbl. **15**: 48. 1940.

DISTRIBUTION: Western part of the Amazon Valley.

A small tree which differs from *Herrania nitida* principally in having smaller and lanceolate-elliptic or very narrowly obovate leaflets, in having a fewer-flowered inflorescence, in having flowers which are usually larger

and redder (the ligules usually entirely red), in having a smaller fruit (7.5–8 cm. long, 4 cm. in diameter), and in being humbler in stature.

Brazil. AMAZONAS: Rio Jutahy, Riosinho Jurunema, *Fróes 21040*. **Colombia.** PUTUMAYO: Umbría, alt. 325 m., *Klug 1853*. AMAZONAS: Trapécio Amazónico, Río Loretoyacu, *Black & Schultes 46–331*. **Peru.** LORETO: Río Ucayali, *Tessmann 3287*; Guamitanacocha, Río Mazán, alt. 100–125 m., *Schunke 45* (Type).

The very striking difference in size between the leaves and nearly all other parts of *Herrania nitida* and *H. nitida* f. *sphenophylla* cannot be laid to ecological variation. When this difference was first noted (on the basis of *Schunke 45*) it was recognized as varietal. Later studies in the field, however, as well as information obtained through an examination of additional collections, indicate that the concept is probably better treated as a form, since little other than color and size differences, constant though they be, are evident.

In 1940, Diels described *Theobroma Mariae* f. *minor* from the Río Pastaza in eastern Ecuador. The type specimen seems to have been destroyed during the recent war. If we may judge from the few characters given in Diels' original description and from geographical distribution, it might be safe to assume that the concept represented either *Herrania nitida* or, more probably, *H. nitida* f. *sphenophylla*. In 1943, I pointed out this possibility (Caldasia 2: 332. 1944), stating: "I have been unable to examine herbarium material or photographs of this form, and, until an opportunity to do so presents itself, I shall be unable to treat it critically. In most of the characters enumerated in the original description, it would seem that . . . it approaches *Herrania nitida* var. *sphenophylla*, although, of course, no mention is made of the fundamentally important character of leaf-pilosity."

13. **Herrania nycterodendron** R. E. Schultes, Caldasia 2: 21. *tt. pag. 22, 26.* 1943; Bot. Mus. Leafl. Harvard Univ. 14: *t. 35.* 1950.

DISTRIBUTION: Westernmost parts of the Amazon Valley.

Small, slender, graceful tree up to 25 feet tall, the trunk usually simple, erect, terete, apically leafy, up to 8–9 cm. in diameter at the base, covered with an ashy-yellowish, scrobiculate bark. Leaves large, 7-digitate, stipulate, very long petiolate. Stipules caducous, linear, acute, 2.5–4 cm. long, more or less 3 mm. wide, dry, tomentose. Petiole strong, terete but very obscurely sulcate, basally slightly swollen, subferruginous, extremely densely and softly tomentose, up to about 60 cm. in length, 8–9 mm. in diameter. Leaflets sessile, unequal lanceolate-oblong, with a rather acute cusp up to 2 cm. long, basally long- and gently decurrent-attenuate, entire (or minutely and obscurely subundulate) but often very conspicuously armed with the hirsute spinule (up to 1 mm. long) formed by the prolongation of the veins; firmly chartaceous or papyraceous, the central leaflets up to 60 cm. long, 22 cm. wide, above dark green and subnitid, subglabrous or very sparsely and minutely hirsute, minutely tomentulose

along the principal veins, beneath pale green, softly stellate-pilose, very densely and softly ferruginous-tomentose along the main nerves; the veins prominently raised on both surfaces but especially so beneath. Inflorescence fasciculate, up to 40-flowered. Flowers cauline, long-pedicellate, in contracted racemes on the lower portions of the trunk. Pedicels very slender, appressed-tomentose, articulate, 2–2.5 cm. long, basally with a short, linear, apically acute bract which is densely tomentose and 3 mm. long. Bud subglobose, large, about 7–8 mm. in diameter, densely and minutely stellate-puberulent, brown. Calyx subcymbiform, divided almost to the base. Sepals 3, strongly unequal, thick, brownish-purple, valvate in the bud, externally minutely stellate-pilose, internally very minutely puberulent; the outer sepal broadly rotund-obovate, apically rotund-obtuse, entire, 19 mm. long, 15 mm. wide; the inner 2 elliptic, entire, apically subacute, about 15 mm. long, 7–8 mm. wide. Petals 5, basally sessile, widely rotund, concave, apically strongly cucullate, 10 mm. long, 8–9 mm. wide, glabrous, muricate-papillose on both surfaces but especially so on the outer, pale yellow with 7 purple nerves, ligulate. Ligules filiform, hanging, membranaceous, glabrous on both surfaces but basally minutely granulose, 2 mm. wide at base, up to 90–100 mm. long, dark purplish with prominent black nerves. Staminal tube 5-parted; stamens alternately 2- and 4-antheriferous, the filaments glabrous, slender and free. Staminodes conspicuous, petaloid, reflexed, lanceolate-elliptic, acute, entire, 19–21 mm. long, 7–9 mm. wide, muricate-granulose on both surfaces. Ovary sessile, ellipsoid, 10-costate and 5-locular, densely pilose, 3 mm. long, 2 mm. in diameter, yellow. Style filiform, glabrous, apically profoundly divided into 5 parts. Stigmas 5, thick. Fruit ellipsoid, 10–12 cm. long, 4–5 cm. in diameter, apically long and gradually attenuate, often slightly constricted near the tip, apically acute or often rotund-obtuse, basally indented and pedunculate (peduncle woody, up to 4–5 cm. long, 3–4 mm. in diameter), with an extremely dense and minute velvety-stellate indumentum on all parts, without stinging hairs, very profoundly 10-costate, with 5 thick and strongly blunt-rounded primary ribs and 5 similar but smaller secondary ribs; pericarp thick-crassulent, sublignose, ashy-yellow when ripe. Seeds up to about 100, triangular or triangular-ovate in outline, flattened, 9 mm. × 8 mm. × 2 mm. thick, in a white pulp.

Brazil. AMAZONAS: Rio Solimões, Fonte Boa, *Fróes 20578*.

Colombia. AMAZONAS: Trapécio Amazónico, Río Amazonas, Leticia, *Schultes 6017*; interior regions of Trapécio Amazónico, between Amazon and Putumayo watersheds, alt. about 400 m., *Schultes 6777*; path near Quebrada Agua Negra (headwaters of Río Hamacayacu), *Black & Schultes 46–389*; Río Loretoyacu, *Schultes 6335*; Río Caqueta, La Pedrera, *Anglo-Colomb. Cacao Coll. Exped.* (*Baker & Cope*) *14*, *20*. CAQUETÁ: Río Caucaya, Laguna Primavera, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *93*; Río Caguán, Cartagena, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *108*; Camp Two, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *110*; Camp Three, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *113*; Camp Four, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *109*; Río Caquetá, at confluence with

Río Caguán, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 121*; Camp Six, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 128*; Piedra Blanca, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 131.*

Peru. LORETO: Río Putumayo, Remanso, alt. 180 m., *Schultes 4011* (Type); Florida, north of Río Zubineta, alt. 200 m., *Klub 2069*; "Corbata", opposite Isla Salamanca, alt. 180 m., *Schultes 4012*; near Caucaya, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 97*; Río Amazonas, Mishayacu, near Iquitos, alt. 100 m., *Klug 1588.*

Herrania nycterodendron most closely resembles *H. Mariae* and *H. Cuatrecasana.* It is immediately set apart from these species, however, by its curious type of fruit. The fruit of *Herrania nycterodendron* has a dry, somewhat coarse and fibrous rind which is covered completely with a soft indument of velvety hairs; it lacks the stinging hairs which are usually present in this genus. The ribs of the fruit of *Herrania nycterodendron* are broad and rounded with deep furrows. The fruit is apically much more bluntly rounded, in most cases, than is that of related species.

Fróes 20578 is a sterile collection which has been referred to *Herrania nycterodendron* with some reserve.

The natives of the Peruvian bank of the Río Putumayo near Remanso, Isla Salamanca, refer to *Herrania nycterodendron* as "bat-tree" or "tree of the bats". This curious common name may be due, as several natives explained to me, to the fact that the soft, velvety indument of the fruit feels like the fur of small bats which are common in the vicinity. It may also be due to the fact that the fruits cluster on the basal portions of the stem in such a manner as to suggest bats which are accustomed to pass the day hanging from the lower parts of the trunks of small trees in the dark forests. The Witoto name, *mu-sĕ'-na*, is also applied to the *marraca* (*Theobroma glauca* Karst.), and *mu-sé-ge-ke,* the diminutive, is very commonly used to refer to *Herrania nycterodendron* and possibly also to *H. Mariae* var. *putumayonis.*

14. **Herrania pulcherrima** Goudot, Ann. Sci. Nat. III. 2: 232. *t. 5, figs. 11, 12.* 1844.

Theobroma pulcherrima (Goudot) De Wildeman,[5] Pl. Trop. Grande Cult. 89. 1902.

DISTRIBUTION: The mountainous regions of Central Colombia.

Small tree up to 15–24 feet tall, with a simple, columnar trunk 15–25 cm. in diameter. Bark thin, ashy-brown, scrobiculate, glabrous except near the apex where it is covered with a ferruginous indument. Branchlets villose, obscurely sulcate. Leaves 10–15, large, digitate, very long-petiolate, 5–7-foliate. Petioles robust, terete or sulcate, very densely ferruginous-villose, as long as the leaflets, 7–10 mm. in diameter. Leaflets sessile, unequal, lanceolate-ovate, marginally coarsely and regularly sinuate towards

[5] This combination has been made independently by later workers, apparently unaware of the earlier publication. *Cf.* Pittier, Man. Pl. Usuales Venez. 147. 1926.

the apex, acuminate, basally attenuate, very coriaceous, mostly 45–60 cm. long (occasionally much longer), 19–35 cm. wide; above dark green, shining, coarsely muricate or minutely subtuberculate, glabrous (or extremely remotely armed with caducous hairs), the nerves minutely but densely tomentulose; beneath brownish green, densely and softly ferruginous stellate-pilose, softly and densely villose-sericeous along the veins. Stipules caducous, linear, tomentose, 3 cm. long. Inflorescence fasciculate, many-flowered (20–30). Pedicels 11 mm. long, 1.2 mm. in diameter, scabrid-hirtellous and minutely stellate-pilosiusculous. Buds ovoid, densely fulvo-tomentose, 10 × 6 mm. Flowers large, crimson-red. Calyx subcymbiform. Sepals 3, subchartaceous, broadly ovate or elliptic-ovate, entire, rounded or subacute, externally brownish red, stellate-tomentose and stellate-puberulent, internally glabrous and crimson-red, up to 19–20 mm. long, 12–13 mm. wide, valvate in the bud. Petals 5 or (usually) 6, sessile, obovate, concave, strongly cucullate muricate-papillose or granulose on both sides, but especially externally, longitudinally striate-veined, the 5 veins prominently purple or black internally, crimson or dark red, ligulate. Ligules pendulous, 80–110 mm. long, 2–3 mm. wide, glabrous, strongly marked with 3 dark red veins, basally strongly and abruptly contracted, dark purplish red. Stamen tube 5-parted with alternately 2- and 3-antheriferous stamens and simple, short, free filaments. Staminodes very conspicuous, petaloid, lanceolate-elliptic, apically 3-fid, marginally entire, muricate-granulose on both sides, dark purple-red, 23 mm. long, 7 mm. wide. Pistil up to 7.5 mm. long. Style slender, simple yellow, 3.5 mm. long, the stigmatic tip deeply 5-fid. Ovary sessile, 5-locular, ovoid, very densely pilose, pale yellow, 4 mm. long, 3 mm. in diameter. Fruit ellipsoid, attenuate-acuminate, 10-costate, with 5 large primary and 5 smaller secondary cultriform ribs, covered, especially along the ribs, with minute stinging stellate hairs, the rind very thin when dried but crassulent in life, yellow when ripe. Seeds probably about 50, compressed, triangular in outline, in a sweet white pulp.

Colombia. META: Iraca, San Juan [de Arama], Llanos Orientales, *Goudot s. n.* (Type). BOYACÁ: region of Mount Chapon, northwest of Bogota, El Umbo region, alt. 3,000 ft., *Lawrence 437*. CUNDINAMARCA: Municipio de El Peñon, Hacienda "Curiche," alt. 1000 m., *Jaramillo 202*.

The type specimen of *Herrania pulcherrima* has always been thought to be in Paris, but, as in the case of *H. albiflora,* there is material in Geneva which may well be the true type from which Goudot's description and illustrations (at least of the flowers) were made. Goudot spoke of the type plants as inhabiting the great forests situated between the Ríos Ariari and Guayabero, affluents of the upper Orinoco, in the Colombian *llanos*.

The Geneva material consists of two sheets. It is labelled in Goudot's hand, "*Herrania pulcherrima* mihi. An. Sc. Nat. 1844. Llanos del Orinoco, pueblo d'Iraca, San Juan, Flos: Dec." One sheet consists of a piece of golden-tomentose stem about one foot long, a very young leaf, and young

capsules. One of the envelopes has the native Coreguaje Indian name (reported by Goudot in the original description): "*cacao cahouai* — Llanos". Another envelope, on the outside of which Goudot has written "C N. 2 theobroma affinis *Herrania pulcherrima*," has a completely and beautifully dissected flower, the separate parts glued to the inside of the envelope. There can be no doubt but that Goudot made his drawing of the flower of *Herrania pulcherrima* (loc. cit. *t. 5, figs. 11, 12*) from this same dissection.

The leaf which is preserved at Geneva could not have served as a basis for Goudot's excellent description, but a study of the material and the description would seem to indicate that the Paris material represents that from which the original description of the leaf was drawn.

It may be of value to publish a few notes on Goudot's dissection of the flower. The three sepals are laid flat, the very slightly puberulent inner surface exposed. Two are rather broadly ovate, about 15 mm. long and 5 mm. wide (all measurements taken dry), apically rounded; the third, somewhat elliptic, 18 mm. long and 4 mm. wide, apically bluntly pointed. The five petals are all about equal, strongly cucullate, very densely muricate-papillose or granulose externally, papillose internally in six longitudinal lines, the ligules up to 90 mm. long, 2.5 mm. wide immediately above the constriction at its junction with the petal. The staminodes are lanceolate-elliptic, 15 mm. long, 4–4.5 mm. wide, muricate-granulose, and apically so strongly trifid that the tip appears to be mucronate. This was noted by Goudot when he described the staminodes as apically "mucronés et échancrés;" but, in his drawing, he indicated the tip as extremely acute. The ovary is very densely yellowish tomentose.

It is unusual to find a species of *Herrania* which occurs both east and west of the Andes, as well as in the valley between the several Andean chains in Colombia. Yet that appears to be the distribution of *Herrania pulcherrima*. Goudot said that he had found it in the deep valleys of the eastern Andean chain, near Savana-Grande and Payme where, however, it seemed to be rare and isolated. I have seen no Goudot specimen from this locality, but it is very significant, I think, to note that all earlier and a number of the later collections were made not in the eastern llanos but within the *Andean* cordillera.

Vegetatively, *Herrania pulcherrima* can easily be confused (and has been confused) with *H. tomentella*, a species growing in the eastern llanos at the foothills of the Andes where the type of *H. pulcherrima* was collected. The differences between these two species are discussed under *Herrania tomentella*.

The earliest reference to *Herrania pulcherrima* is Eloy Valenzuela's minute description of the plant written in Mariquita in the Departamento del Tolima, Colombia, in 1784, while he was engaged in the work of the Mutis Botanical Expedition in New Granada. For historical reasons, this description has been reproduced in full under the generic description at the beginning of the synopsis.

In the collection of Mutis plates, there is a most strikingly beautiful and accurate water-color of a section of *Herrania pulcherrima* in full flower.

A number of diagnostic characters of this species are most clearly shown: the congested, many-flowered inflorescences, the very abbreviated pedicels, and the long and membranaceous ligules with alternate scarlet and whitish bands. Of this colored plate, there are two copies in black and white. No foliage seems to have been drawn. A search in the Mutis collection of plants in Madrid has failed to produce a specimen of *Herrania pulcherrima*.

The specific name *pulcherrima*, meaning "very beautiful," could not be more appropriate. It recalls Valenzuela's picturesque remark, which I have used as a theme for this synopsis; that the flower of *Herrania pulcherrima* or *cacao esquinado* "could be considered as the greatest marvel of the plant kingdom, and one can hardly believe that nature, as frugal and simple as she is, would have used so many ribbons and so much ornamentation to adorn herself almost as ostentatiously as in the fashions".

14a. **Herrania pulcherrima** Goudot var. **pacifica** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 131. *t. 28, lower fig.* 1950.

Herrania pacifica Cuatr. Rev. Acad. Col. Ciénc. Exact. Físic. Nat. 7. **27**: 307. 1947. Nomen nudum.

DISTRIBUTION: Pacific coastal slope of Colombia and northern Ecuador and the Gulf of Urabá in Colombia.

A small tree up to 25 feet tall, differing from *Herrania pulcherrima* chiefly in having strongly membranaceous leaflets which are minutely stellate-pilose and not muricate or subtuberculate above; lateral leaflets usually strongly oblique; flowers which are commonly much smaller, with the petals and ligules yellow or white; and smaller fruit (11.5 cm. long, 7 cm. in diameter).

Colombia. ANTIOQUIA: north of Dabeiba, road to Turbo, *Univ. Calif. 3rd Bot. Exped. Andes 1942 (Metcalf & Cuatrecasas) 30173*; near Guapá, 53 km. south of Turbo, alt. about 50 m., *Haught 4607*; Urabá, Municipio de Mutatá, Villa Arteaga, alt. about 150 ft., *Schultes & Cabrera 18707a.* VALLE: Pacific Coast, Río Yurumangui, Caimanero, *Cuatrecasas 16010*; Río Calima, Quebrada La Brea, alt. 30–40 m., *Schultes 7324.* CHOCÓ: Río San Juan, vicinity of Palestina, alt. 0–30 m., *Cuatrecasas 21337*; Río Andaquedá, Lloro, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 174.* **Ecuador.** PICHINCHA: Santo Domingo de los Colorados, alt. 800 m., *Acosta-Solis 10923*; "foot of western cordillera", alt. 100 m., *Rimbach 48.*

This concept, as indicated by the varietal epithet, would seem to represent a western or Pacific coastal variant of *Herrania pulcherrima*, a species which, in its typical form, is endemic to the Cordilleras of Colombia.

15. **Herrania purpurea** (Pitt.) R. E. Schultes, Caldasia **2**: 333. 1944; Caldasia **3**: 23. *t. pag. 24, fig. 1, 2.* 1944; Bot. Mus. Leafl. Harvard Univ. **13**: 282. 1949.

Theobroma purpureum Pitt., Fedde Rep. Sp. Nov. **13**: 319. 1914; Standl. Contr. U. S. Nat. Herb. **27**: 262. *t. 51.* 1928; Standl., Contr. Arnold Arb.

5: 104. 1933; Standl., Field Mus. Nat. Hist. Bot. Ser. Publ. 392: 688. 1937; León, Inst. Interam. Ciénc. Agríc. Bol. Técn. 2: 6. 1949.

DISTRIBUTION: Costa Rica, Nicaragua, Panama and northwesternmost Colombia.

Small tree up to 10 feet tall, without branches along the trunk, except near the apex, with grey bark becoming glabrous but densely yellow-villose when young. Leaves usually 5-digitate, stipulate. Stipules linear, acute, dark purple, more or less stellate-villose, caducous, up to 5 cm. long, 3 mm. wide. Petioles terete, obscurely sulcate, somewhat ferruginous-villose, strong, basally rather swollen, 30–45 cm. long. Petiolules strong, very short, up to 5 mm. long. Leaflets unequal, obovate-oblong, basally cuneate, apically broadly and obtusely acuminate, entire or very obscurely sinuate, thin-chartaceous, glabrous above, sparsely and minutely stellate-villose beneath (the nerves densely stellate-villose on both surfaces), almost as long as the petioles, 22–35 cm. long, 6–13 cm. wide. Inflorescences fasciculate, 5–8-flowered. Flowers cauline, in contracted racemes on the lower and middle portions of the trunk, dark purple, pedicellate. Pedicels terete, articulate, brown-tomentose, about 4 mm. long, basally subtended by a short, linear, naviculiform bract which is densely brown-tomentose externally, glabrous internally. Buds globose, 7–9 mm. in diameter, villose. Calyx patelliform. Sepals 3 (rarely 4), united for half their length, broadly ovate or (rarely) elliptic-ovate, obtuse, entire, 12 mm. long, 9 mm. wide, brownish purple, glabrous within, ferruginous, densely stellate-tomentose without. Petals 5, sessile, obovate, strongly cucullate, up to 8 mm. (frequently less) long, 4 mm. wide, muricate-papillose on both sides but denser externally (especially along the nerves), pale purple without, veins deep purple within, longitudinally striate-nerved, 5-veined, ligulate. Ligules linear, very narrowly lanceolate, basally emarginate, acute, hanging, dark purple, about 15 mm. long, 1.8–2 mm. wide. Staminal tube 5-parted, short, 3 mm. long; stamens alternately 1- and 2-antheriferous; filaments simple, short, free; anthers about 1.5 mm. long, longitudinally dehiscent, yellow. Staminodes petaloid but not very conspicuous, ovate, apically acute, reflexed, densely muricate-granulose, red-purple, 9 mm. long, 8 mm. wide. Ovary ovoid, 10-sulcate, villose, 2.5 mm. long, 1.3 mm. in diameter. Style glabrous, 5-parted. Fruit not numerous, elliptic-ovoid, often irregularly twisted, up to 9 cm. long, 5 cm. in diameter, apically rotund-obtuse, slightly constricted near the apex, basally hardly indented, with a strong, comparatively long, peduncle, 10-costate, the 5 primary and the 5 secondary ribs almost equal, blunt-rounded, 5 mm. and 4 mm. high, respectively, and very densely armed with stinging stellate hairs, between the ribs striate-fibrous and armed with stinging hairs; pericarp crassulent-coriaceous or subligneous, yellow when ripe. Seeds 25, obtusely rhomboid, flattened, about 1 cm. long, 1.3 cm. wide and up to 0.6 cm. thick.

Colombia. ANTIOQUIA: Golfo de Urabá, region around Turbo, road between Turbo and Río Grande, *Schultes 5754*; Río Micurí, *Schultes 5755*; Municipio de Pavorandocito, outskirts of Pavorandocito, alt. 80 m., *Gutiérrez 2000*; Mu-

nicipio de Mutatá, Villa Arteaga, alt. about 150 ft., *Schultes & Cabrera 18653, 18593*; *Schultes & López 10464*; *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *164, 169, 170.*

Costa Rica. Palmar, Río Grande de Terraba, *Pittier & Durand 3926, 6721*; Pacific Coast, Boca Culebra, alt. 50 m. *Pittier 12158.* Limón: La Colombiana Farm of United Fruit Company, alt. about 70 m., *Standley 36832*; Finca Montecristo, Río Reventazón, below Cairo, alt. about 25 m., *Standley & Valerio 48421, 48545, 48584*; Hamburg Finca, Río Reventazón, below Cairo, *Standley & Valerio 48792*; hills above tramline, Los Negritos Farm near Río Reventazón, *Dodge & Neverman 7178.* Golfo Dulce: Playa Blanca, *Valerio 461.*

Nicaragua. *Seemann s. n.*

Panama. Monte Lirio, *Hayes 398.* Canal Zone: Near El Paraíso, alt. 30–100 m., *Pittier 2574*; forests along Río Indio de Gatún, *Maxon 4835*; Valley of Masambí, road to Las Cascadas Plantation, alt. 20–100 m., *Pittier 2675*; Barro Colorado Island, Gatún Lake, *Maxon, Harvey & Valentine 6804, Kenoyer 443*; Gatún Lake, *Standley 31319*; alt. 120 m., or less, *Standley 40911*; Armour House to second bay north, *Bangham 549, Bailey & Bailey 31, Shattuck 198*; near end of Fairchild Trail, *Wetmore & Abbe 73*; hills north of Frijoles, *Standley 27434*; Gamboa, *Standley 28416*; near Fort Randolph, *Standley 28647*; Obispo, *Standley 31722*; near Madden Dam, *Alston 8861.* Chiriquí: Progreso, *Cooper & Slater 283.* Bocas del Toro: Laguna de Chiriquí and vicinity, *Hart 96, von Wedel 1112*; Changuinola Valley, *Dunlap 448, von Wedel 976, 1721, Lucas 2.* Darien: trail between Pinogana and Yavisa, alt. 15 m., *Allen 282.* Panamá: vicinity of Caña, alt. 900 m., *Goldman 1974*; Changuinola, *Cooper & Slater 12a*; Changuinola and Sixaola, *Rowlee & Stock 1029*; Marraganti and vicinity, alt. 10–200 ft., *R. S. Williams 662.*

Herrania purpurea is obviously most closely allied to *H. albiflora*, a relationship which is discussed under *H. albiflora*. Both species are alone in the genus in having a curious patelliform calyx and extremely short ligules which give the flowers an entirely different appearance from those of all other species which have a subcymbiform calyx, usually with very long, filiform ligules. *Herrania albiflora* and *H. purpurea*, therefore, are considered to form a distinct section of the genus.

Further study may indicate that *Herrania purpurea* might better be treated as a variety of *H. albiflora*; but, at the present state of our understanding, the two would seem to represent well established specific concepts which geographically are sharply delineated.

Herrania purpurea is the only species of the genus known to occur outside of South America. It has its main center of distribution in lower Middle America but it is represented in the adjacent part of Antioquia (and probably in the northern Chocó) — the northwesternmost corner of Colombia.

The binomial *Herrania purpurea* was published as a *nomen nudum* in the first edition of Thomas Belt's "The Naturalist in Nicaragua" (1874, p. 116). Belt wrote: "About here grows a cacao (*Herrania purpurea*) differing from the cultivated species (*Theobroma Cacao*)." I have been unable to discover a description of the plant or a publication of the binomial prior to 1874. In the preface of his book, Belt stated that "Prof.

D. Oliver of Kew has kindly named for me some of the plants." In the collection of *Herrania* at Kew, I did not find any specimen from Nicaragua collected prior to 1874 and annotated with this binomial. Dr. N. Y. Sandwith of Kew has kindly searched through the archives and reports that he can find nothing which might suggest that Oliver had published the binomial.

Pittier's description of *Theobroma purpureum* was based upon a Panamanian collection, and he made no mention of a prior publication of this specific epithet. There is no doubt that the binomial which Belt published refers to the same concept which Pittier later and independently described and for which he used the identical specific epithet. In accordance with the International Code of Botanical Nomenclature, therefore, we must consider Pittier's *Theobroma purpureum* as the first valid use of the specific epithet.

According to Pittier (Fedde Rep. Sp. Nov. 13: 319. 1914; Standley, Field Mus. Nat. Hist. Bot. Ser. 18 (Publ. 392): 688, 1937), the Bribrí Indians of Costa Rica employ the roasted seeds for preparing a bitter drink.

16. **Herrania tomentella** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 16: 205, 213. *t. 32.* 1954.

Herrania nitida (Poepp.) R. E. Schultes var. *aspera* (Karst. & Tr. ex Tr.) R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 130. 1950, *pro parte.*

DISTRIBUTION: Eastern foothills of the Andes in the Orinoco drainage area of Colombia.

A small tree, slender and graceful, commonly up to 12 feet in height. Trunk erect, about 3 inches in diameter, covered with blackish bark, sparsely branched near the top or unbranched. Branches tomentose. Branchlets densely villose, with golden-rust-colored and persistent hairs. Leaves very large, digitate, 7-foliate, very long-petiolate. Petioles round, somewhat constricted at the base, very densely and softly golden or ferruginous, tomentellous, up to 60 cm. long, 9–10 mm. in diameter. Stipules persistent, linear, densely rough-tomentellous, up to 3 cm. long, 2 mm. wide. Leaflets sessile, oblanceolate or broadly lanceolate-ovate, erect, strongly unequal, membranaceous to papyraceous, acuminate, basally attenuate, the margin both regularly and lightly sinuate-dentate in the upper half but especially towards the apex and everywhere armed with cilia-like stellate hairs, 30–50 cm. long, 13–20 cm. wide, above rough to the touch with sparse, single, brown hairs, beneath rather softly and densely tomentellous with long golden-rust-colored stellate hairs. Inflorescence fasciculate, relatively few-flowered, growing from the lower portion of the trunk. Pedicels articulate, 7 mm. long, 1.5 mm. in diameter, densely stellate-pilose. Buds globose, 15 mm. in diameter, densely stellate-pilose. Calyx 3-parted, divided almost to the base, subcymbiform. Sepals commonly unequal, rather carnose in life, dark purplish, strongly valvate in the bud, externally rather coarsely stellate-pilose, internally very minutely granulose-pulverulent; the 2 interior sepals round-ovate, the margins entire,

apically perfectly rounded, about 14 mm. long, 10 mm. wide; the exterior sepal usually triangular-elliptic, the margin entire, apically subacute, 13–14 mm. long, basally 6–7 mm. wide. Petals 5, basally sessile, obovate or ovate, apically very strongly concave-cucullate, about 8 mm. long, 7 mm. (often up to 8 mm.) wide, dark blood-red with purple nerves, externally minutely muricate-verrucose, ligulate. Ligules linear, about 70 mm. long, basally 3 mm. wide, filiform near the apex, dark blood-red but near the tip pinkish. Staminal tube 5-parted with stamens bearing 1 and 2 anthers alternately and with short, free filaments. Staminodes petaloid, dark blood-red, membranaceous, elliptic, marginally entire, acute, 14–15 mm. long, 6–7 mm. wide, somewhat verrucose on both surfaces. Fruits not numerous, ellipsoid, up to 9 cm. long, 4 cm. in diameter, long-attenuate but near the tip slightly constricted, the tip itself obtuse and frequently twisted, basally not indented, pedunculate, with remnants of the persistent sepals; peduncle articulate, 3 cm. long, 4 mm. in diameter, everywhere densely and very minutely velvety-pilose, soft to the touch and without stinging hairs, very deeply 10-costate, the 5 primary ribs thick and bluntly rounded, 8 mm. high, the 5 secondary ribs similar but smaller, 4–5 mm. high, transversely rather fibrous-rugose, the pericarp thick, almost woody, reported to ripen yellow. Seeds about 60, embedded in a white pulp.

A description of the pollen grain of *Herrania tomentella* is given under the generic description at the beginning of this monograph.

Colombia. [No precise locality], *Rocha s. n.* META: Villavicencio, alt. 300 m., *Triana s. n.*; *Sprague 135*; Sierra de la Macarena, Playa Bonita, alt. 400 m., *Philipson, Idrobo & Fernández 1420*; Caño Entrada, alt. 550 m., *Philipson, Idrobo & Jaramillo 2199*; Sabanas de San Juan de Arama, Río Guëjar, near landing-field Los Micos, alt. about 500 m., *Idrobo & Schultes 612, 721*; path between Río Guëjar and Caño Guapayita, alt. about 500–600 m., *Idrobo & Schultes 787, 1192* (Type); Caño Yerly, *Schultes 11629*; Sabanas de San Juan de Arama, Río Guëjar, *Schultes 11821.*

Herrania tomentella resembles, in its foliage, *H. pulcherrima* and *H. Cuatrecasana*. It differs from the former in having a much more finely sinuate margin, in having a smooth (instead of a rather muricate-subtuberculate) upper surface, in being more finely tomentose beneath, and in being membranaceous (rather than coriaceous) and generally smaller. From the latter, it can be distinguished by differences in the shape and margin of the leaflets: those of *Herrania Cuatrecasana* are conspicuously long attenuate-decurrent towards the base and have very remotely and obscurely crenate-denticulate margins.

In form of the fruit, *Herrania tomentella* approaches *H. Cuatrecasana* more closely than *H. pulcherrima*. The capsule of *Herrania pulcherrima* has strongly cultriform ribs with stinging hairs, whereas that of *H. tomentella* has broadly rounded ribs without stinging hairs. Furthermore, floral differences between *H. pulcherrima* and *H. tomentella* are marked, especially in the staminodes which are apically trifid in the former but acute in the latter.

Although there are a number of resemblances between the capsule of *Herrania tomentella* and that of *H. Cuatrecasana*, the soft indumentum and lack of stinging hairs in the former are in sharp contrast to the condition in the latter where, except for stinging hairs along the ribs, the surface is glabrous or glabrescent. There are likewise several floral differences.

The leaflets of *Herrania tomentella* are borne in a partly erect position. This is also true of *Herrania Cuatrecasana* and *H. pulcherrima* and possibly of all species which have a noticeably swollen callus at the base of the leaflets. In this erect position of the leaflets, *Herrania tomentella* differs strikingly in habit from the only other species known in the Macarena, *H. nitida*, which has leaflets which tend to be rather reclinate.

A study of the fruit of the material from the Macarena has clarified a confusion of long standing. Although in the past specimens of *Herrania tomentella* have been referred to *H. pulcherrima* or to *H. nitida* (as *H. aspera* or *H. nitida* var. *aspera*), a study of the capsule, until recently unknown, shows conclusively that *H. tomentella* has its relationships in other directions. The history of the confusion between *Herrania tomentella* and *H. aspera* has been discussed in detail under the heading of *H. nitida*.

17. **Herrania umbratica** R. E. Schultes, Caldasia 2: 261. *t. pag. 263, figs. a–d.* 1943; R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 86. *t. 24.* 1955.

DISTRIBUTION: Department of Santander, Colombia.

Small, slender, graceful tree up to about 16 feet in height, with the branches grouped at the top of the trunk. Trunk erect, up to 15–18 cm. in diameter, the bark probably brownish black; the root long, fusiform. The branchlets densely ferruginous-tomentose. Leaves very large, 7-digitate, very long-petiolate, stipulate. Stipules membranaceous, 3–6 cm. long (according to the collector). Petioles strong, sub-terete but obscurely sulcate, slightly swollen near the base, rusty, densely but softly tomentose, up to about 60–65 cm. long, basally 10 mm. and apically 4–5 mm. in diameter. Leaflets unequal, sessile, papyraceous, lanceolate-oblong, rather acutely cuspidate with a tip about 2 cm. long, basally subattenuate-cuneate, entire; above dark green and almost glossy glabrous, minutely and obscurely ferruginous-tomentose along the main veins, beneath of almost the same color, very minutely and sparsely stellate-pilose, the nerves prominent and rather more densely stellate-pilose; the central leaflet 55–60 cm. (according to the collector, 40–70 cm.) long, 20–22 cm. wide; the lateral leaflets smaller. Inflorescence fasciculate, many-flowered. Flowers cauline, arising from the lower part of the trunk in abbreviated racemes, short-pedicellate. Buds globose in anthesis, 18–22 mm. in diameter. Pedicels up to 5 mm. long, densely fulvo-tomentose, articulated basally and subtended by a minute, linear bract. Buds globose, mostly 10–12 mm. in diameter. Calyx patelliform, obscurely 2-parted. Sepals very fleshy, 2, connate most of their length, subequal, rotund-ovate, entire, apically rounded, more or less 22 mm. long, 22 mm. wide, glabrous and

purple within, without yellow-brown and very densely and minutely stellate-pilose and sparsely and coarsely stellate pilose. Petals 5, sessile, thick, blood-red, concave, obovate, mostly 9 mm. long, 8 mm. wide, apically stongly cucullate, within with 5 thick-callused, purple, muricate-papillose veins, glabrous between the nerves but near the thickened margin densely muricate-papillose. Ligules linear, 19 mm. long, 2 mm. wide at base, the base strongly and abruptly contracted, spirally twisted in the bud but in flower erect, yellowish red, minutely granulose. Staminal tube 5-parted, the stamens 2- and 4-antheriferous, with short, free, strongly flattened filaments; anthers 2-locular, the locules 1.5 mm. long, 0.6 mm. wide, yellow. Staminodia thick, conspicuously petaloid, yellowish, strongly deflexed, hiding the petals and anthers, oblanceolate-elliptic, entire, apically subacute, 20 mm. long, 10 mm. wide, densely papillose-granular on both surfaces. Ovary sessile, elongate-ovoid, 10-costate and 5-locular, reddish golden, very densely stellate-pilose, 3 mm. in diameter. Style fleshy-terete, simple, yellow, apically conspicuously 5-parted into a stigma, 1 mm. long. Fruits numerous, up to 45 to a tree; elongate-ellipsoid, conspicuously irregular, mostly 11–14.5 cm. (according to the collector, up to 17 cm.) long, 4.5–5 cm. (according to the collector up to 8 cm.) in diameter, apically rotund-obtuse, not constricted near the apex, basally obtuse (not indented) and pedunculate (with a woody, articulated peduncle up to 10 mm. long, 4 mm. in diameter), with 10 subequal ribs, the 5 primary ribs thick, irregular, blunt-rounded, 6–8 mm. high, 5 mm. wide, the secondary ones similar but rather smaller, about 5 mm. high, 5 mm. wide, somewhat striate-fibrous between the ribs, very sparsely and rather grossly beset with simple, white, probably stinging hairs up to 1.5 mm. long, lacking a velvety indumentum; pericarp crassulent-leathery or subligneous, 3–4 mm. thick; bright yellow when ripe. Seeds 45, triangular or angular-ovate in outline, flattened, 13 mm. × 10 mm. × 3 mm., in a white pulp, measuring 18 mm. × 15 mm. × 7 mm. with the pulp.

Colombia. SANTANDER: Municipio de Girón, region of Capitancitos, alt. 695 m., *Ortíz Méndez s. n.* (Type). NORTE DE SANTANDER: Río Tibú, above Beltrania, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *179*; Río Orú, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *180*; Río Nuevo, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *182*. **Trinidad.** Imperial College of Tropical Agriculture, *Baker s. n.*

When *Herrania umbratica* was originally described, the resemblance of its fruit to that of *H. nycterodendron* led to the suspicion of some relationship between the two concepts. Further investigation, however, has indicated that *Herrania umbratica* and *H. albiflora* are probably very closely allied.

The vegetative differences between *Herrania umbratica* and *H. albiflora* are slight. *Herrania albiflora* f. *titanica* would seem to represent, in some respects, a link between the two species. Exact relationship, however, cannot be established, until complete flowers of *Herrania umbratica* and additional fruits of *H. albiflora* are found. In the present state of our

knowledge, we may say that the fruit of *Herrania umbratica*, similar in some respects to that of *H. nycterodendron*, differs from the fruit of *H. albiflora* (as represented in Goudot's line drawing published with the original description of *H. albiflora* and as known for *H. albiflora* f. *titanica*) in being irregularly contorted (instead of very regular); in having the primary and secondary ribs nearly equal and so thick that there is little flat intercostate area (instead of having the primary ribs twice or more higher and much thicker than the secondaries and extensive flat areas between the ribs); in being apically extremely thick and blunt (instead of having a slender, somewhat attenuate tip which is but slightly obtuse); and in having the peduncle much stouter than that of *H. albiflora*.

Further investigation and additional collections may possibly indicate that *Herrania umbratica* would better be considered as a variety of *H. albiflora*, but a complete understanding of the floral structure of *H. umbratica* must be had before any definite decisions can be made in this respect.

The collector of the type of *Herrania umbratica* records that this same species is found in townships in the vicinity of Girón, the type locality: San Vicente, Lebrija, Zapatoca, and Betulia. There are, however, no specimens from these localities. Regarding the habitat of *Herrania umbratica*, Ortíz Méndez wrote in his field notes: ". . . loose sandy, sandy-clay soils . . . the normal growth of the plant occurs in rather wet situations . . . it grows and develops in the shade of the trees which are known in the region by the names *juanblanco*, *canalete*, *guarumo*, *guamo*, *anaco*, *barba de mono*, *cocotinajo*, *qualanday*, etc." Of diseases which attack *Herrania umbratica*, he reported: "The trunk and branches are completely healthy. There are sporadic cases of insect attack to the fruits, but these attacks do not harm the seeds. Fungal attack is absolutely negative. The leaves are attacked slightly by *crisomélidos* and *minadores*."

PLANTS OF UNCERTAIN POSITION

THEOBROMA MARIAE (Mart.) K. Schum. f. MINOR Diels, Notizbl. **15**: 48. 1940. The possible position of this concept is discussed under *Herrania nitida* f. *sphenophylla*.

THEOBROMA MONTANA Goudot ex Bernoulli, Neue Denkschr. allg. Schweiz. Gesell. gesam. Naturw. **24**: 15. 1871, nomen nudum. Under the caption: "species mihi ignotae," Bernoulli published this name without a description and without the citation of specimens. It may represent a species of *Herrania*, for Bernoulli commented: "Vero similiter *Herraniae* species."

HERRANIA GUIANENSIS Sagot ex K. Schum. Mart. Fl. Bras. **12**(3): 75. 1886. Nomen in syn. French Guiana. "Karouany", *Sagot* (?) *s. n.* When K. Schumann published as a synonym of *Theobroma speciosum* Willd. ex Spreng. Sagot's manuscript name *Herrania guianensis*, he cited Sagot *1206*, a collection from French Guiana consisting merely of flowers. In the Utrecht herbarium, I found specimen number 000030 to be a collection of flowers only. They represent *Theobroma speciosum*, but on the outside of the packet there is a handwritten

annotation: "*Herrania guianensis* Sagot". This is probably part of the Sagot collection cited by Schumann.

COMMON AND NATIVE NAMES KNOWN FOR THE SPECIES OF HERRANIA

In compiling the following enumeration of names used for *Herrania* in Middle and South America, I have included all orthographical variants which have been found in the literature. The list is made up from the literature, from labels on herbarium specimens and from my own ethnobotanical observations in the field. In each case, the country or countries in which the name is employed has been indicated. Some of the names reported are taken from the Indian languages, in which cases it has almost always been possible to designate the specific tribe.

abare	Venezuela: (Musuchíes Indians)	*H. lemniscata*
a-no-kwa	Colombia: (Kubeo Indians)	*H. nitida*
a-wa-ka-de-ro	Colombia: (Kuripako Indians)	*H. nitida*
awarivacabariyek	Venezuela	*H. lemniscata*
bee-ay-o	Colombia: (Makuna Indians)	*H. nitida*
be-se-o-wa	Colombia (Tanimuka Indians)	*H. nitida*
boscacao	Dutch Guiana	*H. kanukuensis*
bur-oo-ma	British Guiana: (Arawak Indians)	*H. lemniscata*
cacahuillo	Perú	*H. nitida*
cacahuio	Perú	*H. nitida* f. *sphenophylla*
cacaita	Venezuela	*H. albiflora*
cacao cahouai	Colombia	*H. pulcherrima*
cacao cahouit	Colombia	*H. pulcherrima*
cacao cahousí	Colombia	*H. pulcherrima*
cacao caimán	Colombia	*H. Mariae*, *H. nitida*
cacao canaludo	Colombia, Ecuador	*H. Cuatrecasana*
cacao cimarrón	Costa Rica	*H. purpurea*
cacao cuadrado	Colombia	*H. pulcherrima*
cacao de andirá	Brazil	*H. Mariae* var. *putumayonis*
cacao de ardilla	Panamá	*H. purpurea*
cacao de chimbe	Colombia, Perú	*H. nycterodendron*
cacao de cintillas	Colombia	*H. laciniifolia*
cacao de macaco	Brazil	*H. Camargoana*
cacao de mico	Costa Rica	*H. purpurea*
	Colombia	*H. Camargoana*
cacao de monte	Brazil	*H. Mariae*
	Colombia	*H. albiflora* & f. *titanica*, *H. breviligulata*, *H. Cuatrecasana*, *H. Dugandii*, *H. laciniifolia*, *H. Mariae*, *H. nycterodendron*, *H. tomentella*
	Ecuador	*H. balaensis*, *H. pulcherrima* var. *pacifica*
	Panamá	*H. purpurea*
	Perú	*H. nitida*, *H. nycterodendron*
cacao de murcielago	Colombia, Perú	*H. nycterodendron*
cacao esquinado	Colombia	*H. pulcherrima*
cacao maní	Panama	*H. purpurea*
cacao montarás	Colombia	*H. albiflora*
cacao montaráz	Colombia	*H. albiflora*
cacao jacaré	Brazil	*H. Camargoana*, *H. Mariae*, *H. Mariae* var. *putumayonis*

cacao quadrado	Brazil	*H. Mariae*
	Colombia	*H. pulcherrima*
cacao silvestre	Colombia	*H. laciniifolia*, *H. Mariae* var. *putumayonis*, *H. nitida*
	Perú	*H. nitida*, *H. nycterodendron*
cacao simarrón	Colombia	*H. albiflora*
cacao symarrón	Colombia	*H. albiflora*
cacaoito de monte	Colombia	*H. nitida*, *H. pulcherrima*
cacaorana	Brazil	*H. Mariae*
caca-ú	Brazil	*H. Mariae*
cacau de quina	Brazil	*H. nycterodendron*
cacauí	Brazil	*H. Mariae*
cacau-jacaré	Brazil	*H. Mariae*
cacau-rana	Brazil	*H. Mariae*
cahouit	Colombia	*H. pulcherrima*
cha-te-ra	Colombia, Perú: (Tikuna Indians)	*H. nitida*
chocolatillo	Panamá	*H. purpurea*
coco del monte	Panamá	*H. purpurea*
ee-so-pe-ke	Brazil: (Tukano Indians)	*H. Camargoana*
hee-ree-la-na-pee-ta-re	Colombia: (Yukuna Indians)	*H. nitida*
he-me-ka-ra	Colombia: (Taiwano Indians)	*H. nitida*
jo-kee-kee-yo-ke	Colombia: (Kubeo Indians)	*H. nitida*
ko-kee-ot-chu	Colombia, Ecuador: (Kofán Indians)	*H. Cuatrecasana*, *H. nitida*
ku-ra-ta	Colombia: (Karijona Indians)	*H. nitida*
maipoilie doron doron	Dutch Guiana: (Karib Indians)	*H. kanukuensis*
ma-mi-ree	Colombia: (Kabuyari Indians)	*H. nitida*
maripoele kakaoeleo	Dutch Guiana: (Karib Indians)	*H. kanukuensis*
matayaka	Venezuela: (Maquiritare Indians)	*H. lemniscata*
mi-to-ro-re	Colombia: (Karijona Indians)	*H. nitida*
mu-se-ge-ke	Colombia, Perú: (Witoto Indians)	*H. Mariae* var. *putumayonis*, *H. nycterodendron*
mu-se-na	Colombia, Perú: (Witoto Indians)	*H. Mariae* var. *putumayonis*, *H. nycterodendron*
o-so-pee-ko	Brazil: (Tukano Indians)	*H. Camargoana*
o-yaw-pee-ka-ye	Colombia: (Desano Indians)	*H. nitida*
palo de chimbe	Colombia, Perú	*H. nycterodendron*
palo de murciélago	Colombia, Perú	*H. nycterodendron*
pan y cacao	Colombia	*H. albiflora*
rus-ub	Panamá: (Bribrí Indians)	*H. purpurea*
sacha cacao	Colombia: (Inga Indians)	*H. breviligulata*, *H. Cuatrecasana*
so-pee-ja-ke	Colombia: (Gwanano Indians)	*H. nitida*
tach-ko-au	Colombia: (Miraña Indians)	*H. nitida*
toot-choo	Colombia: (Yurutí Indians)	*H. nitida*
wild cacao	Panamá: Canal Zone	*H. purpurea*
wild cacao	British Guiana	*H. lemniscata*

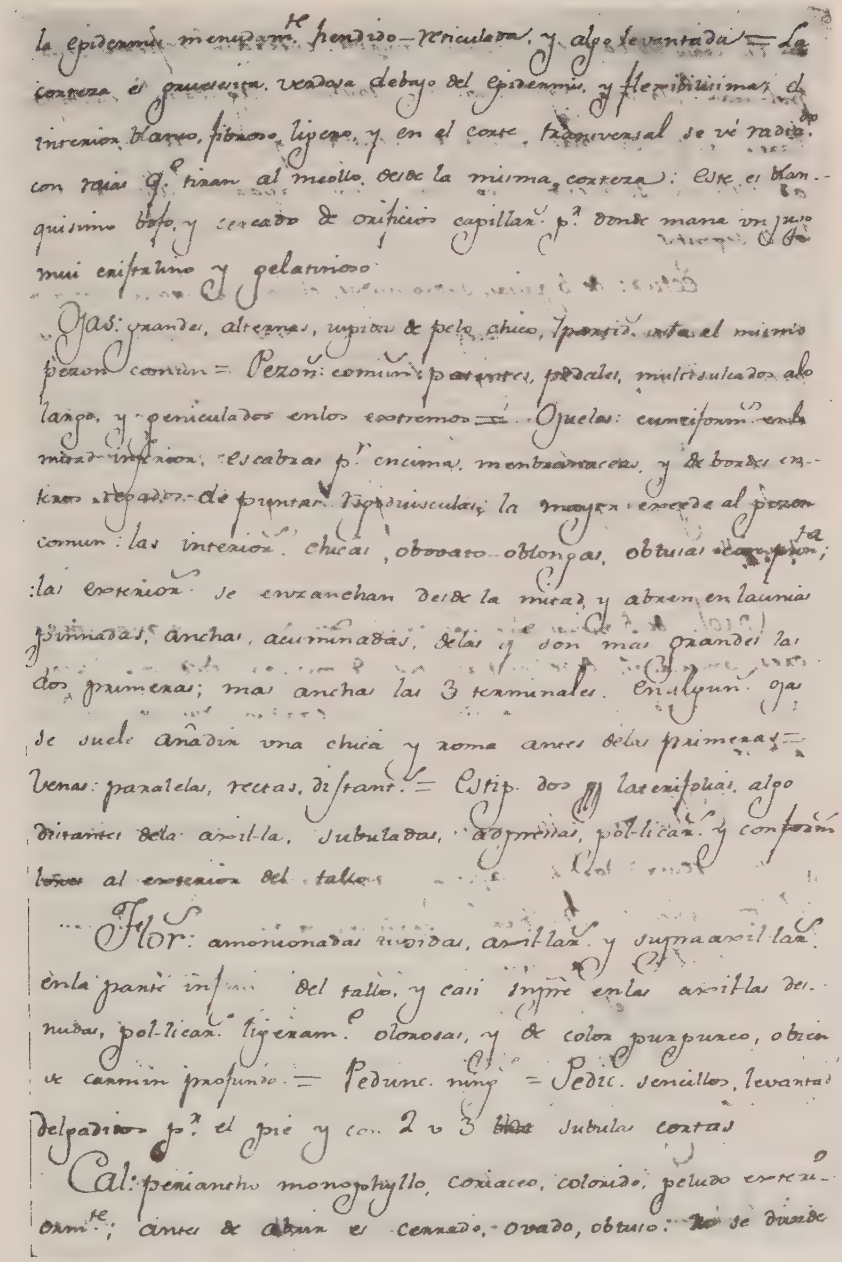
INDEX TO EXSICCATAE

For purposes of facility in consulting material of *Herrania* in our herbaria, the following list summarizing the collections which have been consulted in the preparation of this synopsis is offered. The list is arranged alphabetically by the last name of the collector. Numbers in parentheses refer to the corresponding species in the text.

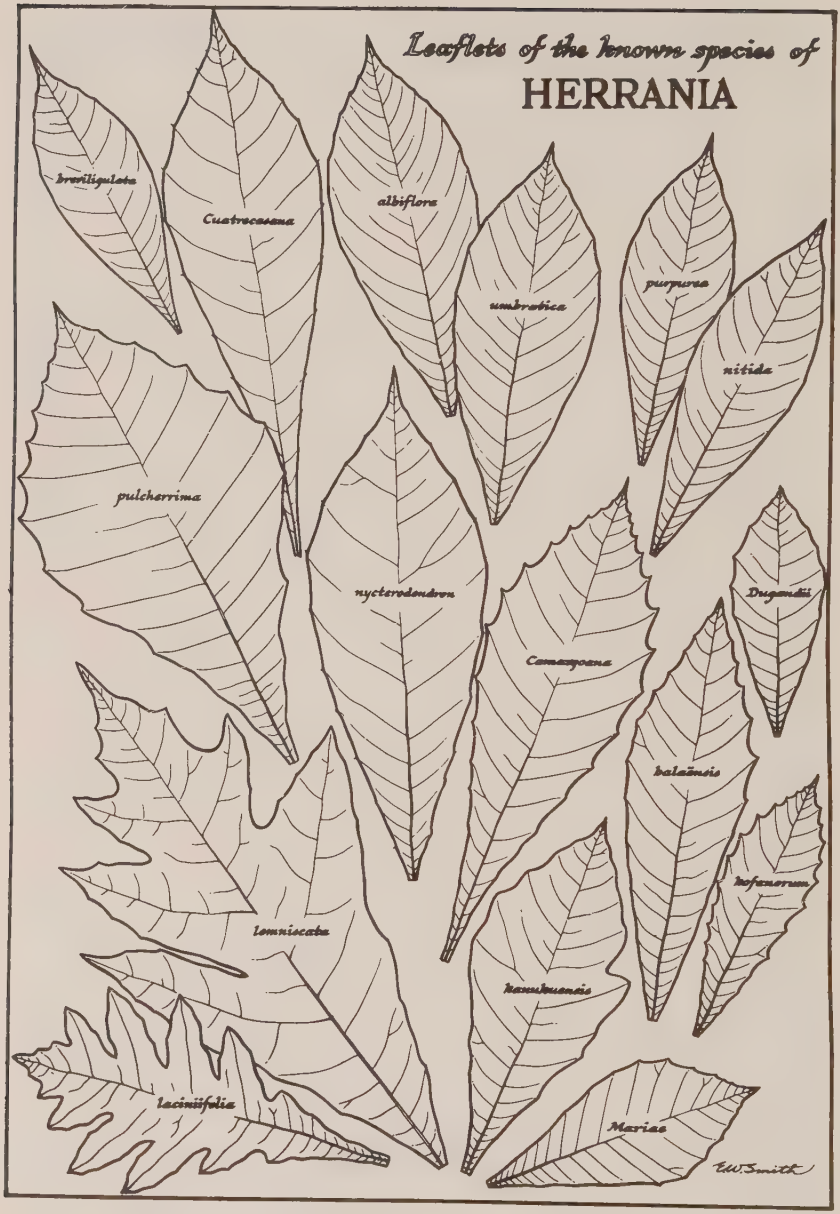
Acosta-Solis *10923* (14a)
Allen *282* (15)
Alston *8861* (15)
André *K 26* (2)
Anglo-Colombian Cacao Collecting Expedition *78* (3); *35*, *39*, *45*, *56* (4); *80*, *84*, *86* (5); *89* (8); *55c*, *67*, *76*, *85*, *87*, *88*, *92*, *100*, *106*, *112*, *120* (12); *93*, *108*, *109*, *110*, *128*, *131* (13); *174* (14a); *164*, *169*, *170* (15); *179*, *180*, *182* (17).
Archer *2514* (10)
Aristeguieta *1598* (1)
Bailey *s.n.* (1)
Bailey & Bailey *31* (15)
Bangham *549* (15)
Bates *s.n.* (16)
Black *47–1916* (11)
Black & Schultes *46–223* (11); *46–331* (12a); *46–389* (13)
Bonpland *1580* (1)
Cooper & Slater *12a*, *283* (15)
Cruz (de la) *3892* (10)
Cuatrecasas *11168* (5); *10742* (6); *16010*, *21337* (14a)
Curran *135* (1)
Dodge & Nevermann *7178* (15)
Ducke *595* (11); *s.n.*, *7618* (12)
Dunlap *448* (15)
Eggers *14362* (2)
Exped. Bot. Mutisii Novae-Granat. *3759* (1); *937* (9)
Forest Dept. British Guiana *F 1764* (10)
Fróes *21468*, *21540*, *22673* (3); *23003* (7); *20630*, *21041* (11); *20919* (12); *21040* (12a); *20578* (?13)
García-Barriga *8375* (9), *14016* (12)
Ginzberger *804* (11)
Glaziou *9635* (12)
Goldman *1974* (15)
Gonggrijp *2111*, *2565*, *4101*, *4117*, *4126* (7)
Goudot *s.n.* (1); *s.n.* (9); *s.n.* (14)
Grassl *10121* (12)
Hart *96* (15)
Haught *1490* (1a)
Hayes *398*, *399* (15)
Hulk *26* (7)
Idrobo & Schultes *768*, *791*, *1325* (12); *612*, *721*, *787*, *1192* (16)
Im Thurn *s.n.* (10)
Jaramillo *202* (14)
Kalbreyer *2047* (9)
Kenoyer *443* (15)
Killip *34247* (12)
Killip & Smith *27431*, *28234* (12)
Klug *1853* (12a); *1588*, *2069* (13)
Krukoff's 4th Exped. Bras. Amazon *4523* (11)
Krukoff's 5th Exped. Bras. Amazon *6085* (12 × 11)
Lanjouw & Lindeman *2304* (7)
Lawrence *437* (14)
Lucas *2* (15)
von Martius *s.n.* (11)
Martyn *61* (10)
Maxon *4835* (15)
Maxon, Harvey & Valentine *6804* (15)
Mexía *7328* (3)
Murça Pires *775*, *1159* (4)
Murça Pires & Black *740* (11); *873* (12)
Myers *3371* (10)
Ortíz Méndez *s.n.* (17)
Pennell *3799*, *3832*, *4208* (1)
Pérez-Arbeláez *10303* (9)
Philipson et al *1420*, *2199* (16)
Pittier *2574*, *2675*, *12158* (15)
Pittier & Durand *3926*, *6721* (15)
Poeppig *1979* (12)
Purdie *s.n.* (1)
Richter *s.n.* (1a)
Rimbach *48* (14a)
Rocha *s.n.* (16)
Rowlee & Stork *1029* (15)
Ruíz & Pavón (?) *s.n.* (12)
Rusby & Squires *252* (10)
Schomburgk *s.n.* (10)
Schultes *18639* (1); *18638* (2); *3342* (5); *6038* (6); *3478*, *3670* (8); *6238*, *6461*, *6759*, *8072* (11); *4010* (11a); *3405*, *3698*, *3730*, *5351*, *5359*, *5491*, *5529*, *5685*, *5715*, *5850*, *5876*, *6000*, *6016*, *6054*, *6058*, *6118*, *6124*, *6141*, *6142*, *6143*, *6144*, *6145*, *6146*, *6147*, *6149*, *6192a*, *6304*, *6383*, *6640*, *6878*, *8129*, *11627* (12); *4011*, *4012*, *6017*, *6335*, *6777* (13); *7324* (14a); *5754*, *5755* (15); *11629*, *11821* 16).
Schultes, Baker & Cabrera *18439*, *18553* (12)
Schultes & Black *8286*, *8377* (12)
Schultes & Cabrera *18720*, *19082* (3); *18712*, *18715*, *18976*, *19100* (5); *13628*,

13630, *13632*, *14343*, *14537*, *14880*, *14882*, *18933*, *19284*, *19665* (12); *18707a* (14a); *18652*, *18693* (12)
Schultes & López *8758*, *8759*, *8762*, *8763*, *8956*, *9144*, *9162*, *9205*, *9240*, *9416b*, *9619*, *9722*, *9747*, *9869* (4); *10464* (15).
Schultes & Murça Pires *8978*, *9130* (4)
Schultes & Smith *2050* (3)
Schunke *45* (12a)
Scolnik, Araque Molina & Barkley *195001* (10)
Seemann *s.n.* (15)
Shattuck *198* (15)
Smith *3541* (7)
Sprague *135* (16)
Spruce *4969* (12)
Stahel & Gonggrijp *3015* (7)
Standley *27434*, *28416*, *28647*, *31319*, *31722*, *36832*, *40911* (15)
Standley & Valerio *48421*, *48545*, *48584*, *48792* (15)
Steyermark *60558* (10)
Tejera *268* (1)
Tessmann *4024* (12); *3287* (12a)
Traill *64* (12); *65* (11a)
Triana *s.n.*, *5333*, *s.n.* (12)
Ule *5031* (11)
Univ. Calif. 3rd Bot. Gard. Exped. Andes *30173* (14a)
Valerio *461* (15)
Von Wedel *976*, *1112*, *1721* (15)
Wetmore & Abbe *73* (15)
L. Williams *11339* (10); *2332*, *2816*, *2843*, *3345*, *3364* (12)
R. S. Williams *662* (15)
Collector unknown [Hort. Trinidad] *s.n.* (1)

Botanical Museum
Harvard University



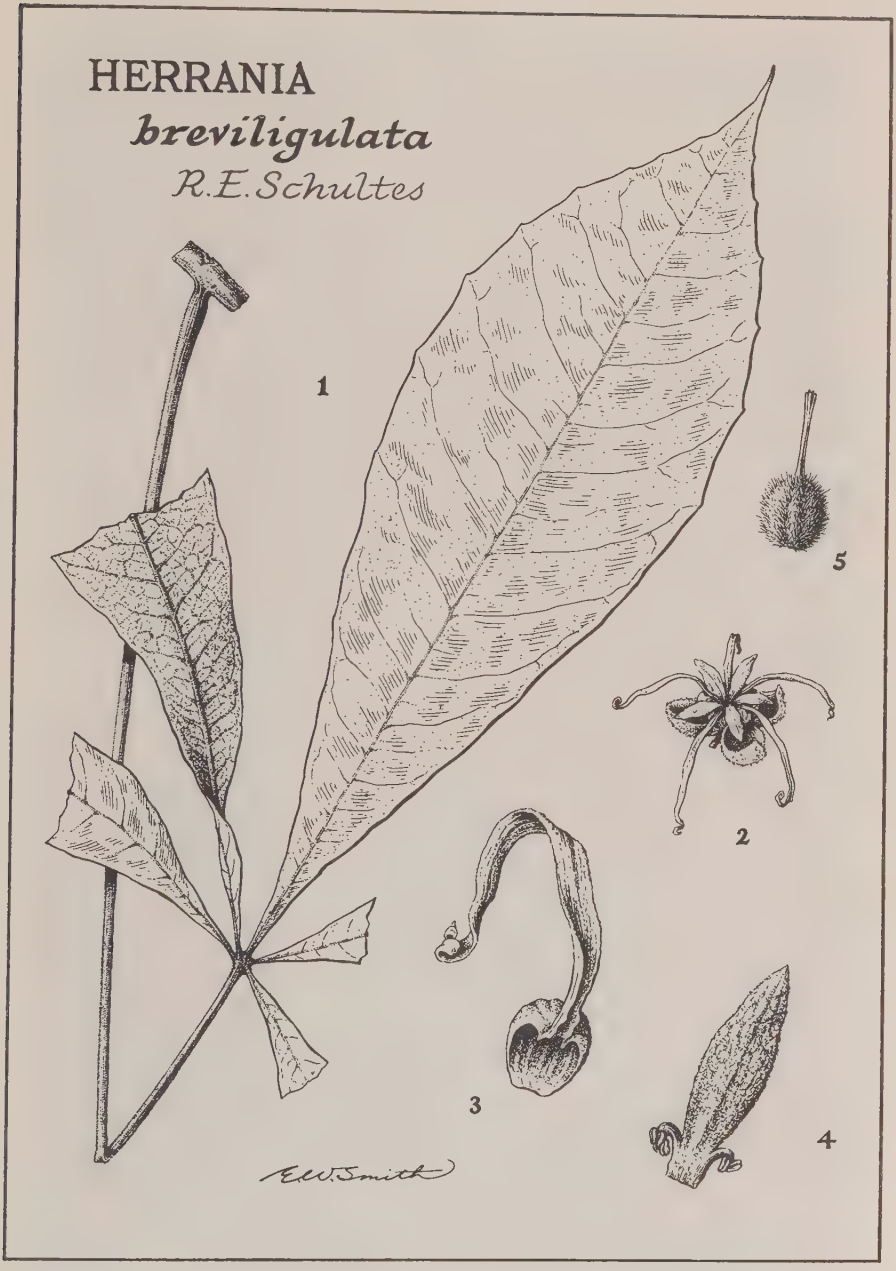
Page of manuscript of Valenzuela's *Diario de la Expedición Botánica al Reino de Nueva Granada* in which the detailed description of *cacao esquinado* (*Herrania pulcherrima*) is set down.



Forms of the leaflets of sundry species of *Herrania*.

Drawing of *Herrania albiflora* from Goudot's original description of the genus and species.

Flower and buds (left) and stipules (right) of *Herrania albiflora*.



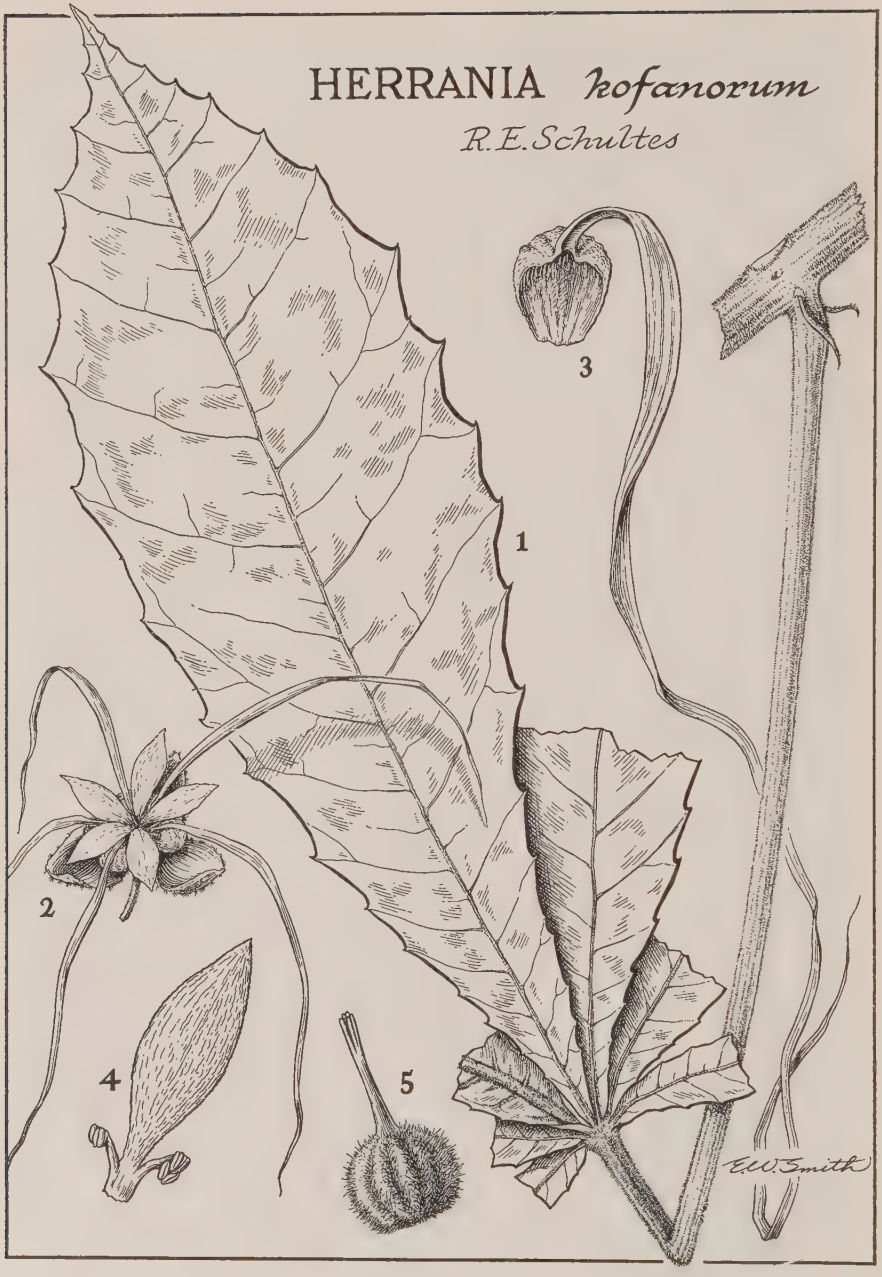
Herrania breviligulata. FIG. 1. Leaf, × 1/3. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Ovary and style, × 4.

Fruits of *Herrania breviligulata*.

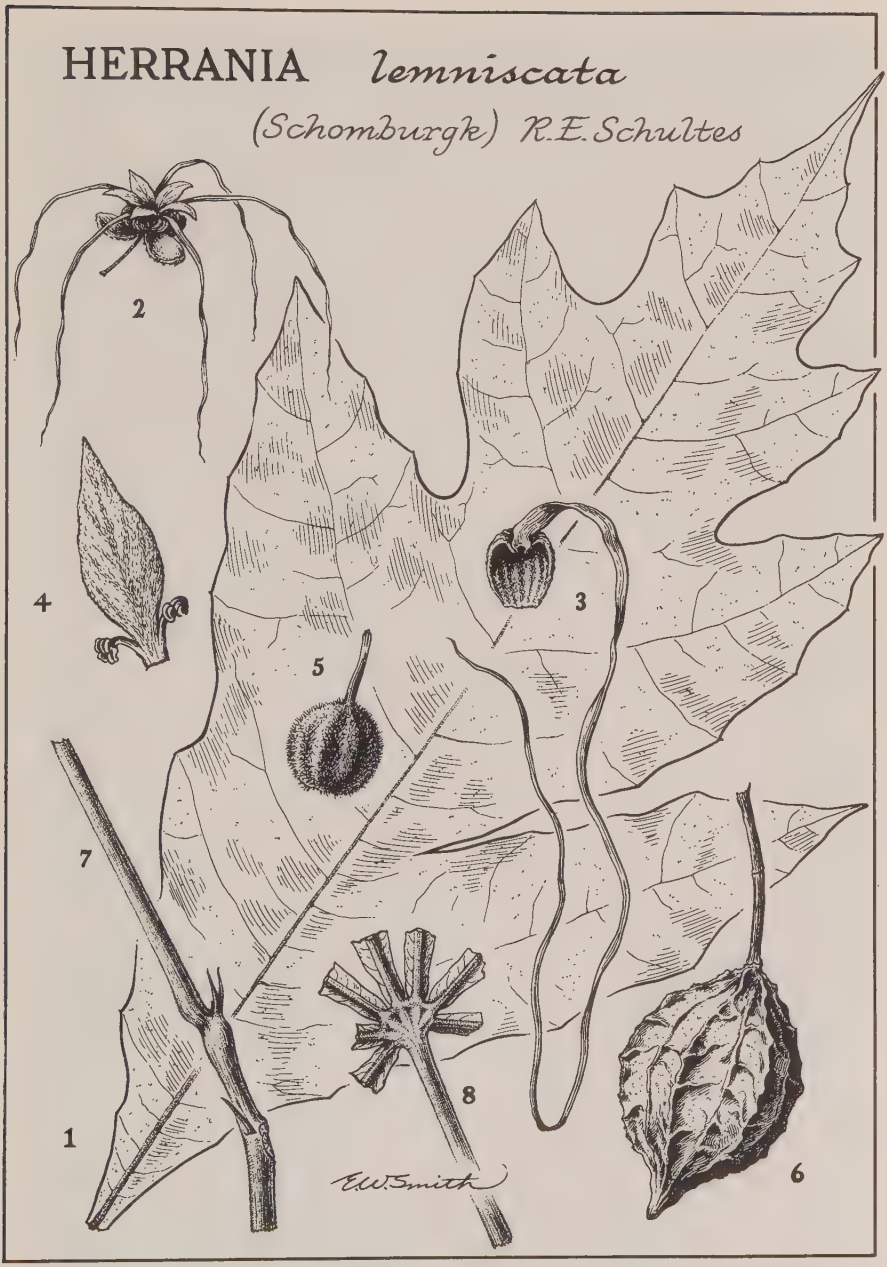
Herrania Camargoana. Fig. 1. Leaf, × 1/4. Fig. 2. Flower, × 1/2. Fig. 3. Petal, × 2. Fig. 4. Staminode and anthers, × 2. Fig. 5. Ovary and style, × 4. Fig. 6. Fruit, × 1/2.

Inflorescences of *Herrania Camargoana*.

Herrania kanukuensis. FIG. 1. Leaf, × 1/6. FIG. 2. Fruit, × 1/2. FIG. 3. Portion of lower surface of leaflet, showing pilosity, × 4.



Herrania kofanorum. FIG. 1. Leaf, × 1/2. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Ovary and style, × 4.



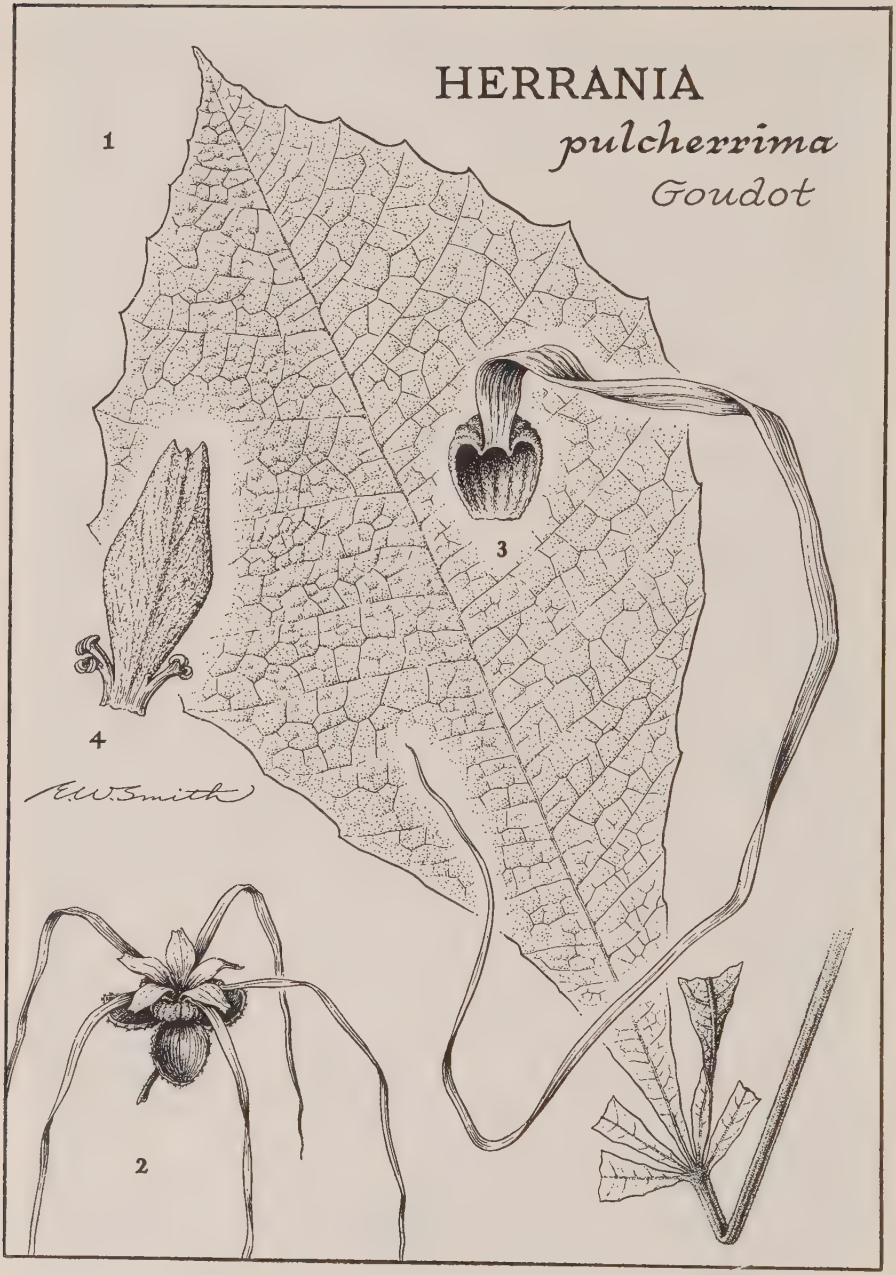
Herrania lemniscata. Fig. 1. Leaflet, × 1/5. Fig. 2. Flower, × 1/3. Fig. 3. Petal, × 2. Fig. 4. Staminode and anthers, × 2. Fig. 5. Ovary, × 2. Fig. 6. Fruit, × 1/2. Fig. 7. Petioles and stipules. Fig. 8. Base of leaflets.

Herrania lemniscata. Schomburgk's field painting of *Lightia lemniscata*, Tab. XLI in the Schomburgk collection of water-colors in the British Museum (Natural History).

Flowers and buds of *Herrania Mariae* var. *putumayonis*.

Fruits of *Herrania nitida*.

Herrania nycterodendron. FIG. 1. Leaf, × 1/4. FIG. 2. Flower, × 1/2. FIG. 3. Staminode and anthers, × 2. FIG. 4. Ovary and style, × 4. FIG. 5. Fruit, × 1/2. FIG. 6. Portion of lower surface of leaf, showing pilosity, × 4.



Herrania pulcherrima. FIG. 1. Leaf, × 1/4. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2.

Herrania purpurea. Fig. 1. Leaf, × 1/3. Fig. 2. Flower, × 1/2. Fig. 3. Petal, × 2. Fig. 4. Staminode and anthers, × 2. Fig. 5. Fruits, × 1/2.

THE GENERA OF THE WOODY RANALES IN THE SOUTHEASTERN UNITED STATES

CARROLL E. WOOD, JR.

THE TREATMENTS PRESENTED BELOW of the sixteen genera of seven woody ranalian families which occur in the southeastern United States have been prepared as part of a generic study of the seed plants of that area. This work has been undertaken as a joint project of the Gray Herbarium and the Arnold Arboretum and has been made possible through the interest and support of George R. Cooley and through a grant from the National Science Foundation. In view of the co-operation and interest others have shown in this undertaking it seems worth while to publish our treatments of at least some of the families in advance of the completed work. In this way some of the material brought together in the course of these studies will be made available, and we should hope to have constructive criticisms from other botanists as the work progresses.

In attempting a generic treatment of the approximately 1300 genera of seed plants known to occur within the area bounded by and including North Carolina and Tennessee, on the north, and Arkansas and Louisiana, on the west, the objectives are toward a review and reorganization of familial and generic lines (often obscured in Small's *Manual of the Southeastern Flora*) and, especially, toward bringing together at least a part of the vast botanical literature which bears upon the plants of this rich area. The work is being done by taxonomists and is both taxonomic and floristic, but the approach, as well as the scope, is intended to be somewhat broader than is usual in a regional manual. The basic scheme is biological with the intent of including material from all branches of botany and of underscoring the biosystematic aspects of each genus and family, insofar as possible. In such an approach more problems may be raised than are solved but, in at least some instances, some of the difficulties which must be resolved before the plants of our area can be understood adequately become evident when the literature of a particular genus or family is brought together. Of course, with the existing information such a large goal is impossible for all genera (or even most) but a biological or biosystematic viewpoint is that which we are attempting to maintain throughout these studies.

The difficulties and weaknesses of this undertaking are apparent to no one more clearly than to those of us who have planned and worked on this project. More than a year and a half were spent on the tedious but basic chore of drawing together a file of more than 50,000 references arranged by families and genera which provided the starting point for the work. The large number of references and their wide distribution in the botanical literature of the world point up the almost incredible amount of information which is rather effectively "lost" to most botanists and even to authori-

ties on particular groups of plants. The amount of material published about some genera of plants (cf. *Magnolia* and *Liriodendron*) is very large, while that concerning others is so scattered and fragmentary that it seems almost impossible to retrace. The matters of locating references, attempting to deal with information from a number of fields, culling, and trying to synthesize in a few choice words the "essence" of the genus sometimes seems to be (and probably is) a nearly hopeless task. The degree of success undoubtedly varies considerably from one group to another, and both sins of omission and commission will be evident. However, the work is absorbing and it is difficult to set aside one group for another, leaving behind many unsolved problems. It is to be hoped that others may take an interest in some of these problems and that the notes and references included will prove to be useful to students and researchers. One thing is certain: there are enough botanical problems in the Southeastern flora to supply all possible workers for a long time to come.

Although the general scheme being followed throughout this work will be apparent in the treatments below, a few explanatory comments will be apropos. It should be noted especially that the descriptions of families and genera are based mainly upon the species which occur in the southeastern United States and are not necessarily wholly applicable to those beyond this area. However, additional information which may provide a more balanced concept of the genus may sometimes be included in brackets. Although each description is regional, the concept of the genus is broader, with an attempt being made to delimit the group more in terms of all its species. Such an approach is essential, for many genera are represented in our area by only a few outlying species which often belong to different sections or subgenera. Were the viewpoint essentially regional these might be placed in different genera to the obscuring of true interrelationships (and to the ensuing confusion of all). This viewpoint is, in general, a conservative one which stresses similarities, rather than differences. In many instances it would seem far better at this stage of our knowledge to point out a problem than to attempt a solution which may only cause ultimate confusion.

The notes included vary widely with the group. Not all branches of botany will be found to be equally well represented: the training and background of the present investigators leads to the emphasis of taxonomic and biosystematic materials, although an attempt has been made to include as much other information as possible. Pathology and palaeobotany, each a large field with its own special and extensive literature, are likely to be represented least well. Limitations of space prohibit the inclusion of the source of each item of information, but a series of selected references will provide many of these. References included are primarily to journals. Many standard texts have been consulted but, rather than to cite each of these repeatedly, it is planned to include a list in the final work. Many references have been annotated as to content, especially when the title is not self-explanatory. Abbreviations used for journals follow the clear and useful general principles followed by Schwarten and Rickett (Bull. Torrey Bot.

Club 74: 348–356. 1947, and a much amplified list now in press) which are in accordance with the recommendations of the Madison Botanical Congress of 1893 and the International Code of Botanical Nomenclature, 1956. Those references which we have not seen are followed by an asterisk (*).

The illustrations are by Dorothy H. Marsh (Mrs. Stephen Marsh) who has worked meticulously in depicting the details upon which the accuracy of scientific illustrations depends. Since the adequate illustration of more than a thousand genera is likely to be quite impossible, the drawings have been planned on the assumption that, even though few in number, illustrations which provide some insight into the details of the plant are far more desirable in a work at the generic level than a larger number of "recognition" drawings. These more detailed drawings, which eventually will represent genera scattered throughout the whole range of families, are being made mostly from fresh or preserved materials as these become available. A number of kind individuals have been most helpful in their efforts in this direction, and the living collections of the Arnold Arboretum, which include many woody plants of authentic southern origin, have provided invaluable material.

The project is under the direction of Dr. Reed C. Rollins and the writer. Dr. Kenneth A. Wilson is working with us at the present time and we have had as our other excellent collaborators Dr. R. B. Channell, now of Vanderbilt University, and Dr. C. W. James, now of the University of Georgia. All three have worked conscientiously on the many tasks directly concerned with the studies on the Southeastern flora: the preparation of files of references, the identification of specimens, the preparation of generic treatments and the supervision of drawings of groups which they have studied. The basic plan of the generic treatments has been modified through the ideas, trials and efforts of all of us. In these studies a great many friends and colleagues from the staffs of our respective institutions, from many parts of the United States, and from other countries, as well, have brought us appreciated assistance. The appropriate time has not yet come, nor would there be here sufficient space to mention each one individually, but to each I am personally most grateful for his help.

The order Ranales, including as it does the most primitive of known living angiosperms, is one of particular interest from an evolutionary point of view. In recent years, the studies of Professor I. W. Bailey and his numerous collaborators and students have elucidated many aspects of the woody members of this group and have stimulated a renewed interest not only in these plants as a group but in the "complete" approach to problems of the interrelationships of higher categories through the use of information from all parts of the plant, rather than that from a single organ obtained by a single discipline. This approach not only has pointed out the many remarkable primitive structures in various members of this order but has emphasized again and again the very different rates at which structures or organs of a plant may have evolved. Hence, any evolutionary

arrangement of families must be an attempt to sum up the degree of relationship with other groups as well as the over-all level of specialization.

The ranalian families included here are those characterized by their predominantly woody habit and by the possession of the characteristic ranalian ethereal oil cells in the tissues of the plant. In our flora this group includes the Magnoliaceae, Annonaceae, Illiciaceae, Schisandraceae, Canellaceae, Calycanthaceae, and Lauraceae. In spite of investigations on these and other ranalian families by numerous authors, a number of families remain to be studied carefully. The interrelationships of all the families of the order are still far from certain, although various related groups have been pointed out. Thus, the Degeneriaceae, Magnoliaceae, Annonaceae, and Himantandraceae form a group of related families within the order; Illiciaceae and Schisandraceae another; Austrobaileyaceae, Trimeniaceae, Amborellaceae, Monimiaceae, Calycanthaceae, Gomortegaceae, Lauraceae, and Hernandiaceae yet another. The relationships of the Canellaceae are undoubtedly with the ranalian complex (presumably with that group of families having monocolpate pollen and tri-lacunar nodes — perhaps Myristicaceae), instead of with the Parietales where they are placed in the Englerian system, but exactly where remains to be seen. I have not attempted to deal at all with the matter of splitting the Ranales (sensu lato) into other orders, retaining all of these families together, instead, and only arranging these groups in this rough way pending the outcome of studies now under way at several institutions.

In connection with these ranalian families Professor I. W. Bailey has given freely and most helpfully of his knowledge of these more primitive angiosperms and Dr. C. E. Kobuski has most kindly read the entire manuscript with a practiced editorial eye. The flowering material used in the illustration of *Illicium floridanum* came through the kindness of Mrs. J. Norman Henry from plants cultivated at the Henry Foundation, Gladwyne, Pennsylvania, and the fruiting specimens through that of Dr. R. B. Channell from Gallman, Mississippi.

MAGNOLIACEAE (Magnolia Family)

Deciduous or evergreen trees or shrubs with simple, alternate, stipulate leaves with pinnate venation, the stipules inclosing the bud and leaving conspicuous encircling scars at each node. Flowers solitary, terminal [or axillary], perfect [except *Kmeria*], all parts free [in ours]. Perianth of 9–15 green, yellow or white tepals in whorls of threes, the outermost whorl sometimes partially differentiated as a "calyx." Stamens numerous, spirally arranged on the elongated receptacle below the carpels, [7–]3(2 or 1)-veined, often poorly differentiated into "anther" and "filament" with four microsporangia (often confluent as two), dehiscing longitudinally; pollen ellipsoidal, monocolpate, the germinal furrow distal. Gynoecium of numerous conduplicate carpels, free [in ours], spirally arranged on the upper part of the receptacle and so closely imbricated and packed as to appear

syncarpous [in ours], the style elongate, vascularized, the ovaries 1-loculed, in both our genera with 2 anatropous 2-integumented ovules at the inner angle of the locule, back to back with the funiculi adjacent. Fruit cone-like [in ours], composed of the imbricated follicles or samaras which are clearly distinct at maturity; seeds 2 in each carpel, each with abundant endosperm and a minute embryo; embryo sac development normal in all known cases; basic chromosome-number 19 throughout the family.

A family of about 200 species in 6–10 genera, the generic lines not well agreed upon, but including *Magnolia*, *Talauma*, *Michelia*, *Manglietia* and *Liriodendron*. The family is bicentric in distribution: all of the genera occur in eastern or southeastern Asia and *Magnolia*, *Talauma* and *Liriodendron* also occur in the New World. Although many of the 80 fossil "species" of *Magnolia* and the 25 of *Liriodendron* are doubtful, the record is sufficient to show that these two genera were formerly of wide distribution in the Northern Hemisphere but have become extinct over most of this area.

The family as here considered does not include *Schisandra*, *Kadsura*, *Illicium*, *Drimys* and its relatives, *Trochodendron*, *Tetracentron*, *Austrobaileya* and other genera which the studies of I. W. Bailey, his collaborators and students have shown clearly to belong elsewhere. Magnoliaceae (sensu stricto) seems to be most closely related to *Degeneria* and *Himantandra*. (See also Annonaceae.) Canright notes, ". . . the tissues and organs of the Magnoliaceae reveal many transitions between the more primitive Degeneriaceae and the slightly more specialized Himantandraceae; yet all three families undoubtedly form a compact alliance within the woody Ranales."

With their woody habit, wood with some primitive features, mostly perfect flowers, numerous and mostly free floral parts with hypogynous and partially spiral insertion, sporophyll-like stamens, monocolpate pollen and ethereal oil cells, the Magnoliaceae are often considered to be among the most primitive living angiosperms. Bailey & Nast in concluding their studies on the Winteraceae (1945) wrote, however, ". . . it is unfortunate that so much attention has been focused upon the Magnoliaceae (sensu stricto) in discussions concerning the origin of the angiosperms, for the seedlings, stems, roots, leaves, stamens, and carpels of these plants all exhibit a relatively high degree of morphological specialization. More primitive and significant ranalian structures are retained by such families as the Winteraceae, Degeneriaceae, Himantandraceae, Trochodendraceae, etc." The detailed studies of Canright bear this out and he concludes, in part, ". . . the evidence in support of the postulated primitiveness of the Magnoliaceae is in some tropical stamen types, plus the occurrence of distal-furrowed monocolpate pollen."

It may be added that Sect. *Tasmania* of *Drimys* (Winteraceae) appears to combine more numerous primitive features than any other known group of angiosperms. However, in spite of its more advanced position on a world-wide basis, *Magnolia* is probably the most primitive genus within the Southeastern flora.

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Key to the Genera of Magnoliaceae

Leaves entire, acute to cordate-auriculate at the base; petals white, green or yellow; stamens without distinct filaments, introrse or latrorse; styles deciduous; the numerous carpels in fruit forming a cone-like follicetum; carpels opening on the abaxial surface, the seeds pendulous by threads, with a fleshy scarlet to pink outer coat. ..... 1. *Magnolia.*

Leaves with 4 or 6 lobes, truncate-emarginate at the tip; petals greenish-yellow with an orange band near the base; stamens with distinct, although thick filaments, extrorse; styles persistent, flat and wing-like; the numerous carpels maturing as a cone-like mass of samaras, each of which falls separately. ..... 2. *Liriodendron.*

Tribe Magnolieae DC.

1. **Magnolia** L. Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 240. 1754.

Trees, or sometimes shrubs, mostly with showy and large flowers, the leaves deciduous to evergreen, entire or sometimes cordate-auriculate at the base. Tepals 9–15, in series of 3, white or green to yellow [pink or purple], similar or the outer 3 sometimes partially differentiated, deciduous. Stamens with filament and connective hardly differentiated, the latter produced into a blunt point [in ours] beyond the anther-sacs (sporangia); anther-sacs 4, linear, opening introrsely or latrorsely. Styles recurved, deciduous, the stigma along the inner face. Fruit a cone-like follicetum of the more or less fleshy imbricated carpels, the individual follicles at maturity clearly separate, dehiscent along the outer (abaxial side), the two seeds hanging by a delicate silky thread of unrolled spiral vessels (from the funiculus and placenta); seeds with a fleshy scarlet to pink outer layer and a hard bony inner layer, both derived from the outer integument. $2n = 38$, 76, 114. (Including *Tulipastrum* Spach.) Type species: *M. virginiana* L. (Named in honor of Pierre Magnol, 1638–1715, Professor

of Botany at the botanical garden at Montpellier, France.) — MAGNOLIA, BAY, CUCUMBER-TREE.

An ancient genus with about 75–80 species, in two centers: about 50 in the Old World (Japan to the eastern Himalayas, south to Java) and about 25 in the New World (eastern U.S., the Greater Antilles, and Mexico to southeastern Venezuela). Dandy divides the genus into 2 subgenera and 11 sections; both subgenera and 4 sections are represented by the 8 species, including 5 varieties, of our area.

Subgenus MAGNOLIA. Anthers dehiscing introrsely; flowers neither precocious nor with a much reduced outer whorl of tepals; leaves evergreen or deciduous. Eight sections, 5 entirely Asiatic, 2 entirely American.

Sect. RYTIDOSPERMUM Spach includes 3 species of Asia and 4–6 of America, all white-flowered and deciduous, with the leaves crowded together near the tips of the branches. *Magnolia tripetala* L., *M. Fraseri* Walt., *M. pyramidata* Bartr., *M. macrophylla* Michx. and *M. Ashei* Weatherby represent this group in our area. *Magnolia macrophylla* and *M. Ashei* are very similar, differing principally in size of plant and shape of fruit, and probably are only varietally distinct. It is also notable that the Mexican *Magnolia dealbata* Zucc., of the mountains of Veracruz to Oaxaca, is hardly distinguishable from *M. macrophylla* and may well be only disjunct populations of that species. All of the species of the section, except *M. pyramidata* and the Mexican plant (as yet uncounted), have been determined to be diploid ($2n = 38$).

Sect. MAGNOLIA (*Magnoliastrum* DC.) includes only *M. virginiana*, the Sweet Bay, of wide distribution from eastern Massachusetts to southernmost Florida, eastern Texas and Arkansas. The species, a diploid ($2n = 38$), is notable for the adnate stipules, leaves glaucous beneath, and very fragrant, small white flowers. Two geographical varieties (var. *virginiana* and var. *australis* Sarg.), based primarily on size of plant and pubescence of branchlets, peduncles and leaves, are currently recognized but need further study.

Sect. THEORHODON Spach is composed of about 15 American evergreen species with stipules free from the petioles. All are tropical in distribution, with the exception of the exceedingly handsome *M. grandiflora* ($2n = 114$) which ranges from southern Florida northward on the coastal plain to eastern North Carolina and eastern Texas and Arkansas. *Magnolia grandiflora* is widely cultivated throughout our region and has escaped in some areas; the exact limits of its native occurrence need to be determined more carefully. Its closest relationships seem to be with the group of species which includes *M. Schiediana* Schlecht., also with 114 chromosomes, and others of Central America southward to the isolated table-top mountains of southeastern Venezuela. The 8 species of Cuba, Hispaniola and Puerto Rico are all closely related, on the other hand, and form a separate subsection. *Magnolia Hamori* Howard, of Hispaniola, is a diploid; other chromosome numbers are unknown.

Subgenus PLEUROCHASMA Dandy. Anthers dehiscing laterally or sublaterally; flowers precocious and/or with a much reduced (calyx-like) outer whorl of tepals; leaves deciduous. Three sections, two entirely Asiatic.

Sect. TULIPASTRUM (Spach) Reichb., with the outer whorl of tepals reduced to a small "calyx," includes only the green- or yellow-flowered *M. acuminata* L. (sensu lato), of eastern North America, and the purple-flowered *M. liliflora* Desrouss., of eastern China. Both are tetraploids, $2n = 76$. *Magnolia acuminata*, the most variable of our species, appears to be composed of three more or less well defined geographical varieties (var. *acuminata*, var. *cordata* (Michx.) Sarg., and var. *ozarkensis* Ashe), but some aspects of its variation deserve further study. (See Hardin.)

No wild hybrids have been found in the genus, although garden hybrids are common. No hybrids between subgenera have been obtained but a number of intersectional hybrids are known, including *M.* × *Thompsoniana* (Loud.) C. de Vos (*M. tripetala* × *virginiana*) and *M. virginiana* × *grandiflora*. The best known hybrid is the intersectional *M.* × *Soulangiana* Soulange-Bodin (*M. denudata* × *liliflora*) ($2n = 95, 114$), which is widely grown in a number of cultivars. All species appear to be proterogynous, the stigmas being receptive just before the flowers open.

Although *Magnolia* retains relatively primitive sporophyll-like stamens, especially in some of the tropical Asiatic species of Sect. *Gwillimia*, the genus is advanced within the family in respect to carpellary features, being surpassed only by *Liriodendron* which has both more specialized stamens and carpels. *Magnolia* is most closely related to *Talauma*: some of the tropical Asiatic species are so similar in flower that fruit is necessary for proper identification.

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Tribe LIRIODENDREAE Reichb.

2. **Liriodendron** L. Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 239. 1754, "*Liriodendrum*."

Large, deciduous trees with long-petioled leaves with conspicuous stipules and very characteristic leaf-blades with 2 lateral lobes near the base (and sometimes 2 smaller above) and 2 at the apex which appears as if cut off abruptly by a broad, shallow notch. Perianth segments 9, deciduous, the 3 outer ones sepaloid, green, glaucous, reflexed, the 6 inner ones in 2 whorls making a campanulate, tulip-like corolla, greenish-yellow, each with an orange band near the base. Stamens numerous (± 30), the filaments stout, narrowed to the broader, apiculate, extrorse anther. Gynoecium of numerous spirally arranged carpels tightly imbricated into a cone-like column as long as the petals; style elongated, broad, flattened and wing-like, constricted to a small, recurved stigmatic crest. Fruit a spindle-shaped cone of closely appressed 2-seeded samaras, these falling separately at maturity leaving the persistent receptacle; seeds with a thin, dry, and leathery testa. TYPE SPECIES: *L. Tulipifera* L. (The name from Greek, *lirion*, lily or tulip, and *dendron*, tree, from the tulip-like flowers.) — YELLOW-POPLAR, TULIP-POPLAR, TULIP-TREE.

An ancient genus formerly of wide distribution in the Northern Hemisphere, now reduced to two very similar species, *L. Tulipifera*, of eastern North America, and *L. chinense* (Hemsl.) Sarg., of a small area in central China (parts of Kweichow, Chekiang, Hupeh, Kiangsi, and Wushan Provinces).

Liriodendron Tulipifera ($2n = 38$), a very handsome and important timber tree, reaches its best development in the rich, hardwood forests of the Appalachians, attaining a maximum height of 200 ft. and a circumference of almost 35 ft. It is distributed from western Massachusetts and southern Vermont to southernmost Ontario, southern Michigan, Indiana, southeastern Missouri, eastern Arkansas, and Louisiana to central Florida.

FIG. 1. **Liriodendron.** a–j, *L. Tulipifera*: a, flowering branchlet, × 1/4; b, flower-bud with stipular bud-scales, × 1/2; c, stamen, abaxial view, × 2; d, unopened anther, filament, and anther after anthesis, cross-sections, pollen omitted, × 6; e, gynoecium, with sepals, petals, and stamens removed, × 1; f, gynoecium, portion of cross-section, with spirally arranged imbricated carpels, ovaries adnate to axis to lower right, increasingly flattened styles toward outside, the locules and stylar canals in black, × 3; g, carpel at anthesis, vertical section, × 1; h, mature gynoecium with many samaras already shed from axis, × 1; i, samara, × 1; j, lower part of samara, vertical section, with aborted ovule (left) and seed with bony coats, abundant endosperm and small embryo, × 2; d, f, g, j, semi-diagrammatic.

The leaves although always unmistakable are extremely variable and most of those described for 25 fossil species may be matched from the existing populations. The faintly fragrant proterogynous flowers of *L. Tulipifera* are provided with copious watery nectar at anthesis, but seem to be visited primarily by bees collecting the abundant pollen.

Liriodendron chinense ($2n = 38$) seems to be generally a smaller tree, (ca. 50 ft.) with slightly different leaves, smaller flowers and smaller and slightly different fruit. The plant is not nearly so hardy as our native species. Apparently no crosses between the two species have been made; such hybridizations should be of great interest in view of the geographic isolation of the parental species and in comparison with similar crosses in *Catalpa* and *Platanus*.

Liriodendron is isolated within the Magnoliaceae with no close relatives.

It is the only genus in the group with a definitely localized stigma, and the manner of vascularization of the ovules is unique in the family.

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ANNONACEAE (Custard-apple Family)

Trees, shrubs [or vines] with alternate, exstipulate, simple, entire leaves with pinnate venation; buds naked, the leaves conduplicate; oil glands present, the plants aromatic. Flowers perfect [in most], hypogynous, regular, axillary [or terminal], usually nodding. Perianth trimerous, generally of 3 small sepals and 6 petals in 2 whorls of 3, the inner smaller [or sometimes lacking]. Stamens numerous, spirally inserted on the receptacle, filament and anther poorly or not at all differentiated, the sterile tip variously modified; sporangia 4, extrorse, opening longitudinally; pollen in tetrads [or single], monocolpate [to acolpate], the germinal furrow proximal. Carpels many–1, usually free but sometimes united by the ovaries at anthesis [and rarely more completely syncarpous]; stigmas terminal; ovules many–1, in 1 or 2 rows along the adaxial wall or basal, anatropous, 2-integumented. Carpels free in fruit and berry-like, or coalescent, forming a fleshy syncarp. Seeds arillate (in ours), with ruminate endosperm and a small embryo. Embryo-sac development normal (Polygonum type) [insofar as investigated], endosperm development cellular.

A tropical family with 75–120 genera and more than 1000 species, many poorly known, and the classification of the family not yet well agreed upon. Represented in our area by *Asimina*, the only extra-tropical genus, and by *Annona*, which reaches subtropical Florida.

The family is distinguished by the exstipulate, simple leaves, the 3 whorls of 3 perianth segments, the numerous more or less fleshy spirally inserted stamens (each with a single vein), the usually numerous carpels, the fleshy fruits, the large seeds with ruminate endosperm, the tri-lacunar nodes with tripartite median trace, and the monocolpate (or derived) pollen with proximal germinal area (evident in those species in which the pollen is shed in tetrads). Anatomical features of wood, stem and leaf are remarkably uniform throughout the family.

It has been agreed generally that the affinities of the group are with the Ranales (sensu lato) but more precise relationships have been a matter of speculation. The anatomical evidence brought together by Vander Wyk and Canright strongly supports the view that the Annonaceae should be most closely allied with Degeneriaceae, Magnoliaceae and Himantandraceae, on a level of specialization above the Magnoliaceae and perhaps roughly comparable with Himantandraceae.

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1. **Asimina** Adans. Fam. Pl. **2**: 365. 1763.

Trees (to 40 ft.), shrubs or subshrubs (ca. 2 ft.). Flowers nodding, axillary on greatly reduced branches, solitary or in pairs, borne on the wood of the preceding season or on the growth of the year, ill-scented or fragrant. Sepals 3 (rarely 4), small, valvate in the bud. Petals usually 6(–8 or sometimes 12), in 2 (or more) series of 3, the outer largest (often very much larger), imbricated, brown or purplish, greenish, white or yellowish, often increasing greatly in size during anthesis. Stamens numerous–10, inserted on the subglobose to nearly flat receptacle; pollen in tetrads. Carpels 15–1, distinct, the styles short, the stigma small; ovules many–6, in two rows or one. Carpels berry-like in fruit (usually one 1–4 maturing) free, banana-shaped or somewhat torulose to ellipsoid or ovoid, the flesh aromatic; seeds flattened to round, many–4, inclosed in a pulpy membranaceous aril. (Including *Pityothamnus* Small and *Deeringothamnus* Small.) TYPE SPECIES: *A. triloba* (L.) Dunal. (The name from *asiminier,* an early French-colonial name for *A. triloba*, this, in turn, from the Indian name *assimin*). — PAWPAW.

Perhaps 10 species, all of eastern North America. *Asimina triloba* (northern Florida to Texas, north to New Jersey, western New York, southern Ontario, Michigan, Illinois, southeastern Iowa and southeastern Nebraska) and *A. parviflora* (Michx.) Dunal (Piedmont and Coastal Plain, northern Florida to Mississippi, north to southeastern Virginia) have the widest ranges; the others are mostly confined to Florida. The genus includes the only truly extra-tropical species in the family. According to Fries, the only close relative is *Stenanona* Standl., of Panama and Costa Rica.

Although the species of *Asimina* range from deciduous trees reaching 40 ft. (*A. triloba*) to low, fusiform-rooted shrubs with dimorphic stems and partly persistent leaves and, although there is considerable diversity in flower-color and petal-shape, -size, and -sculpturing, the group appears to be a natural one. The differences used by Small in segregating *Pityothamnus* and *Deeringothamnus* seem trivial as generic distinctions. The chromosome-numbers of species of the former group are the same as those of *A. triloba* and *A. parviflora* ($2n = 18$) and, even more significantly, vigorous hybrids have been obtained between *A. triloba* and at least "*A.*

obovata" (= A. *grandiflora* (Bartr.) Dunal?) and "*A. angustifolia*" (= *A. pygmaea* (Bartr.) Dunal?), two very different species assigned to *Pityothamnus*. The former hybrid is known to be fully fertile. No such data are available for the two species placed in *Deeringothamnus* (*A. pulchella* (Small) Rehd. & Dayton, of sw. Florida, and *A. Rugelii* Robins., of ne. Florida). Although differing in the nearly flat receptacle (correlated with reduced numbers of stamens and carpels), in the narrow, hardly fleshy petals of nearly equal size, and in the lack of bracts on the peduncles of the flowers, these plants appear to be only the most specialized members of the genus, standing at the opposite extreme from *A. triloba* but connected to it through the "Pityothamnus" group.

Although apparently rather stable in its vegetative and floral morphology, *A. triloba* shows a wide variation in size, color and palatability of fruits. Two general types have been observed: (1) large, yellow-fleshed, highly flavored, early ripening and (2) small to large, white-fleshed, mild-flavored, late or very late ripening fruits. A number of selected clones, propagated by grafting, are in cultivation.

The flowers of all species are proterogynous. The brown or purple flowers of *A. triloba* and *A. parviflora* are reputed to be ill-scented, while those of the white-flowered species, especially *A. pulchella* and *A. Rugelii*, are fragrant. Beetles appear to be involved in pollination. Most species set few fruit; hand-pollination seems to be necessary to obtain a good fruit-set in *A. triloba*.

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2. **Annona** L. Sp. Pl. **1**: 536. 1753; Gen. Pl. ed. 5. 241. 1754.

Trees (deciduous with us) with rather coriaceous 2-ranked leaves, nodding flowers borne on axillary or supra-axillary branches (which may abort producing the effect of either terminal or axillary flowers), and fleshy syncarpous fruits. Sepals small, valvate in the bud; petals rather thick and fleshy, generally whitish or yellowish, the outer whorl larger and alternate with the sepals and valvate, the inner smaller or very much reduced [or lacking] and valvate [or imbricate]. Stamens club-shaped, the tip modified, generally broad and truncate, very numerous and tightly packed, inserted on the hemispherical receptacle; pollen grains in columns of tetrads. Carpels sessile, numerous, on the receptacle, the ovaries free or united at anthesis, the styles generally club-shaped, fleshy, and conspicuous; ovules solitary in each ovary (rarely 2), erect. Carpels coalescent, forming a many-seeded syncarp with a smooth, squamulose or muricate surface, the individual carpels being indicated on the surface by more or less distinctly outlined areoles. Seeds ovate or elliptical, with a thin outer coat and a thin aril. Type species: *A. muricata* L. (The name from *anon* or *hanon*, the native Hispaniolan name for *A. muricata*, but changed by Linnaeus to Latin *annona*, a year's harvest, in preference to the use of a "barbarous" name, but so that the sound might be kept.) — Custard-apple.

A genus of about 110 species assigned to 17 sections, most species tropical American, but about 10 in Africa; several species widely culti-

vated and naturalized in tropical regions; one species native, one sparingly naturalized and several cultivated in subtropical Florida.

Sect. PHELLOXYLON Saff., with ovate petals, the inner valvate, and ovaries connate at anthesis, includes only *Annona glabra* L. ($2n = 28$), the most widespread species in the genus (West Indies, north to the Bahamas and southern Florida, south to southern Brazil, Mexico to Equador; also in Africa from Senegal to the Belgian Congo). Always at low altitudes and associated with abundant moisture, the Pond-apple or Alligator-apple occurs in Florida in the Everglades and coastal areas in shallow ponds, along the borders of small fresh-water streams or on swampy hummocks; in other areas it seems sometimes to be associated with mangroves. The leaves appear in March–April and flowers in April; the edible but not very palatable fruits ripen in November.

Sect. ANNONA, cauliflorous, but also with ovate petals, the inner imbricate, and with free ovaries, is represented in cultivation by *A. muricata* L., the Guanabana or Sour-sop, a favorite tropical fruit only precariously hardy in Florida.

Sect. ATTA Mart., with elongate petals, the inner greatly reduced, includes *A. squamosa* L. (Sweet-sop or Sugar-apple), *A. reticulata* L. (Bullock's Heart) and *A. Cherimola* Mill. (Cherimoya), all in cultivation in tropical Florida, the first naturalized on some of the Florida Keys.

All species are proterogynous. At the time of pollination a sticky fluid exudes from the stigmas, gluing the styles together and providing a receptive medium for the pollen. The members of sect. *Atta* seem to be cross pollinated (by beetles?) but *A. muricata* may be self-pollinated, at least in some areas. Artificial hybrids have been obtained at least between *A. squamosa*, *A. reticulata*, and *A. Cherimola*, and between these species and *A. glabra*. The Atemoya (*A. squamosa* × *Cherimola*) is regarded as a very promising tropical fruit combining the better features of both parents. The chromosome numbers of the 4 cultivated species above have been reported as both 14 and 16. Numerous cultivars, perhaps involving hybridization, are known in various areas of the tropics. Other species are being introduced and tested for their horticultural possibilities.

According to Fries the genus is most closely related to the American genera *Raimondia*, *Rollinia* and *Rolliniopsis*.

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ILLICIACEAE (Anise-tree Family)

A single genus, *Illicium* L., of southeastern Asia and southeastern North America. Although often placed near *Drimys* (Winteraceae) or associated with the Magnoliaceae, its closest relatives are undoubtedly *Schisandra* and *Kadsura* with which it shares similar pollen, the ranalian type of ethereal oil cell, cambiform "mucilage" cells in the phloem, unilacunar nodes, and similar cuticles, stomata and chromosomes, a combination of characters unique within the Ranales. The total evidence from morphology, anatomy and cytology suggests the inclusion of these three genera either in a single family or in two closely related families; it further pro-

vides a strong obstacle to the association of these genera with either Magnoliaceae or Winteraceae. According to the A. C. Smith, "The three genera will probably be treated by future phylogenists as composing a sub-order of the Ranales, coördinate with suborders composed of the (1) Magnoliaceae, Himantandraceae, and Degeneriaceae, (2) Winteraceae, (3) Trochodendraceae and Tetracentraceae, (4) Eupteleaceae, and other combinations of families . . . not yet sufficiently investigated."

Illicium stands apart from the Schisandraceae in its shrubby or arborescent habit, unmodified receptacle, free stamens, vascularized style, comparatively few carpels in a single whorl, single ovule, fruit a single whorl of follicles, unilacunar nodes with a single trace, pseudo-siphonostelic arrangement of the primary tissues, lack of crystal-bearing sclerenchyma, and a specific combination of primitive and specialized anatomical features in the secondary xylem and phloem.

1. **Illicium** L. Syst. Nat. ed. 10. 1050. 1759.

Glabrous evergreen shrubs or small trees with thin-coriaceous, exstipulate, entire, alternate or distally clustered leaves, the blades decurrent on the petioles. Flowers solitary or 2 or 3 together in minute glomerules, axillary or sub-terminal and appearing crowded among leaves toward the tips of branchlets, sometimes bracteolate, subtended by several caducous bracts. Flowers perfect, hypogynous, the parts free. Receptacle convex to short-conical, usually concealed by carpel-bases. Perianth segments numerous (12–15 or 21–33 in ours), several seriate. Stamens numerous (6–7 or 30–38, rarely –50, in ours), 1-seriate or 2- or 3-seriate, erect, with fleshy filaments and basifixed 4-sporangiate anthers introrsely dehiscent by longitudinal slits; pollen tricolpate. Carpels 11–15(–20), free, in a single whorl, each composed of a laterally flattened ellipsoid ovary distally attenuate into an acute style; style vascularized, conduplicate, stigmatic along the upper side along all or most of its length; ovary unilocular, with a single anatropous ovule on the adaxial side near the base. Fruit a follicetum of a single whorl of free, spreading follicles 10–18 mm. long, these dehiscing along the upper side. Seed with a sub-basal hilum, ellipsoid and laterally flattened, 5–7 mm. long, brownish, glossy; endosperm copious, oily; embryo minute, near the hilum. TYPE SPECIES: *I. anisatum* L. (The name Latin, *illicium*, an allurement, in reference to the fragrance of the fruits of *I. verum* Hook f., an economically important species confused by Linnaeus and others with *I. anisatum*.) — ANISE-TREE.

A genus of some 37 species of southeastern Asia and 5 of southeastern North America. Two species, representing each of the 2 sections, occur entirely within our area. Our species are easily recognized by the fragrant (when crushed), thin-coriaceous, more or less evergreen leaves, the red to yellow relatively small flowers with numerous perianth segments, and the very characteristic star-shaped fruit, a ring of follicles.

Section ILLICIUM (*Badiana* Spach), with 13 species in which the inner

FIG. 2. **Illicium.** a–i, *I. floridanum*: a, fruiting branchlet, × 1/3; b, opening bud with carpels receptive to pollen, × 3; c, flower, later stage at shedding of pollen, the carpels connivent, × 1; d, stamens, inner, outer, and an unusual sub-tepaloid form, adaxial views, × 5; e, two carpels on axis, other flower parts removed, × 3; f, carpel, vertical section, to show folded, unfused sporophyll with single ovule, × 10; g, mature carpel, in section, with horny endocarp (striped) and seed with horny outer seed-coat (black) and endosperm (dotted), × 2; h, mature carpel, cross-section, the mature embryo at micropylar end of seed (to right), × 2; i, seed, × 2; f, g, h, semi-diagrammatic. j, *I. parviflorum*: stamens, adaxial view, × 5.

perianth segments are thin, narrowly oblong or ligulate or lanceolate and somewhat lax at anthesis, is represented with us by *I. floridanum* Ellis ($2n = 28$), a very well marked species which ranges from northwestern Florida to eastern Louisiana and northward to central Alabama at low elevations, especially in wet areas (e.g., around bay-heads). The only close relative of this species is the very similar and perhaps conspecific *I. mexicanum* A. C. Smith, of Veracruz and Tamaulipas. Both plants differ from Old World members of the section in their comparatively long pedicels, numerous stamens and brightly colored perianth segments.

The proterogynous flowers of *I. floridanum*, borne from March to May, are showy, deep red or purple, with an intensely unpleasant odor, both features suggestive of pollination by carrion flies. The species is hardy as far north as Philadelphia where, however, it may lose its usually evergreen habit. The leaves were used with those of *Ilex Cassine* as a tea by the Indians of western Florida.

Section CYMBOSTEMON (Spach) A. C. Smith, with 29 species in which the inner perianth segments are fleshy to paper-like, usually ovate to suborbicular and not lax at anthesis, occurs in our area as *I. parviflorum* Michx. ex Vent., a shrub or small tree which appears to be restricted to a few counties (Lake, Marion, Seminole and Volusia) at the headwaters of the St. Johns River in northeastern Florida. With its obtuse leaves, small, yellowish flowers produced in May and June and reduced number of stamens (6 or 7), this species is unlikely to be confused with *I. floridanum*. Beyond our area the section is represented in the New World by *I. cubense* A. C. Smith, of eastern Cuba, and *I. Ekmanii* A. C. Smith, of western Hispaniola.

Illicium verum, Star anise of southeastern China and adjacent Indo-China, provides a volatile oil used as a medicine, a condiment, or in flavoring liqueurs such as absinthe and anisette. The seeds of *I. anisatum* L. ($2n = 28$), of Japan, contain a poisonous alkaloid.

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SCHISANDRACEAE (SCHISANDRA FAMILY)

A family of two undoubtedly closely related genera of climbing vines, *Schisandra* Michx. (ca. 25 species) and *Kadsura* Kaempf. ex Juss. (ca. 22 species), all of eastern and southeastern Asia and Malaysia, with the exception of a single species of *Schisandra* in the southeastern United States. The two genera have numerous features in common with *Illicium* (q.v.) but differ in the scandent habit, unisexual flowers, enlargement of the torus after anthesis, arrangement of the carpels, absence of a vascularized

style, indehiscent drupe-like carpels, unilacunar nodes with three traces, typically eu-stelic arrangement of the primary vascular tissues, relatively primitive type of secondary xylem and presence of crystal-bearing sclerenchyma. Although the group is of great phylogenetic and phytogeographic interest, its economic importance is restricted to the few Asiatic species which occasionally are cultivated as ornamentals.

1. **Schisandra** Michx. Fl. Bor.-Am. 2: 218. 1803, nom. cons.

Monoecious or dioecious (?) woody climbing vines, the leaves simple, petiolate, exstipulate, alternate on long-shoots or congested on short-shoots, the blade oblong-elliptic to ovate or lanceolate, pinnate veined, entire to sinuate or remotely undulate-denticulate. Flowers pedicellate, unisexual, solitary in the axils of caducous bracts or foliage leaves near the base of the annual shoots, sometimes subtended by 2 or 3 minute secondary bracts. ♂ flowers: tepals 9–12 [5–20], free, 2- or 3-seriate, all similar, the largest elliptic to obovate, 5–8 mm. long; androecium a sessile flattened fleshy 5-cleft pentagonal shield, consisting of 5 radiating stamens with the connectives fused into the shield, the anther-sacs borne on the lower margins of the anthers; opening longitudinally; [in other species stamens 4–60, variously aggregated; pollen 3- or 6-colpate.] ♀ flowers: tepals similar to ♂; gynoecium consisting of a receptacle distinctly longer than broad (1.5–3 mm. long), and numerous (12–)20–30 [–120], 3–5-seriate carpels; ovary ellipsoid to obovoid, the wall fleshy, with stigmatic crests produced distally into an acute, unvascularized pseudostyle and proximally into an irregularly oblong appendage; ovules 2(–3) superposed or obliquely superposed, attached to the adaxial wall of the carpel above the base. Fruit with a greatly elongated receptacle (2–3 cm. long, 2–3 mm. diameter), the pedicel remaining slender, the receptacle bearing 7–12 carpels spaced on its surface; carpels becoming berries, usually ellipsoid or subglobose, the pericarp red, fleshy; seeds 2, ellipsoid-reniform, more or less rugulose; endosperm copious, oily; embryo small, near the hilum. (*Stellandria* Brickell, 1803, nom. rejic.) TYPE SPECIES: *S. coccinea* Michx. = S. glabra (Brickell) Rehder. (The name from Greek *schisis*, a cleaving, and *andros*, of a man, in reference to the "fissures" between the anthers.)

About 25 species of eastern Asia (Manchuria southward to northern Indo-China and the Himalayas, Java and Sumatra), a single species, *S. glabra* in southeastern United States, entirely endemic to our area. *Schisandra glabra* apparently is a very rare plant, being rather poorly known from few and widely scattered localities mostly on the coastal plain in southeastern South Carolina, Georgia, western Florida, Alabama, Mississippi, eastern Louisiana, eastern Arkansas and western Tennessee. The outer perianth segments of the flowers, which are produced in May or June, are greenish, the inner ones increasingly bright red, the androecium red, and the anther-sacs yellow. The greatly elongated receptacle which bears the red or scarlet fruits (July–August) is especially noteworthy.

The genus has been divided by A. C. Smith into four sections based primarily on various modifications of the androecium, which in the most primitive section (*Pleiostema*) may be composed of relatively numerous (–60) and essentially free stamens. Our species belongs to section *Schisandra* in which the androecium is highly modified, flattened and shield-like, composed of five united stamens, and presumably representing one of the end-products of the genus. In addition to *S. glabra*, the section includes *S. repanda* (Sieb. & Zucc.) A. C. Smith, of southern Japan and southern Korea, and *S. bicolor* Cheng, of northwestern Chekiang, China. All three are strikingly similar in characters of perianth-segments, androecium and gynoecium and furnish still another example of the now-familiar pattern of disjunction between eastern Asia and eastern North America.

The chromosome numbers of *S.* (§ *Maximowiczia*) *chinensis* (Turcz.) Baill., *S.* (§ *Pleiostema*) *sphenanthera* Rehder & Wilson, and *Kadsura japonica* (L.) Dunal have all been reported as $2n = 28$.

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CANELLACEAE (Wild Cinnamon Family)

A small family of disjunct distribution with five genera of the West Indies, Venezuela, Brazil, East Africa, and Madagascar. The family is notable for the combination of alternate, exstipulate leaves vascularized by 3 traces from 3 gaps, ethereal oil cells throughout the plant, wood with a number of primitive anatomical features, 3 sepals, 4–12 petals in one or more whorls, a monadelphous androecium forming a tube around the ovary with the anthers extrorse, a single pistil with 2–6 parietal placentae, and monocolpate pollen. Although placed in the Parietales in the Englerian system, the relationships to the woody Ranales have been pointed out a number of times. Within that group an affinity to Myristicaceae has been

suggested by several investigators. The family has also been placed by itself in the order Canellales near the Laurales (here included in the woody Ranales).

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1. **Canella** P. Br. Hist. Jamaica 275. *pl. 27. fig. 3.* 1756; Swartz, Trans. Linn. Soc. **1**: 96. 1791, nom. cons.[1]

Small tree, to 8–10 m. with gray bark and obovate to oblanceolate, rounded or emarginate, deep green, lustrous, evergreen leaves. Flowers small, perfect, regular, in terminal and axillary cymose inflorescences. Sepals 3, imbricate, persistent, the petals 5, deep red, connate at the base. Stamens 10, completely united in a tube with the 10 linear extrorse anthers on its outer surface below the summit. Ovary superior, 1-locular with 2 parietal placentae and about 4 semi-anatropous ovules, the stigma 2–3 lobed. Fruit berry-like, red, with 2–4 shining black seeds. Embryo small with a large amount of endosperm. Pollen monocolpate. (*Winterana* L., 1759, nom. rejic.) Type species: *Canella alba* Murr. (= *C. Winterana* (L.) Gaertn.). (Name from Low Latin, *canella*, cinnamon, from Latin,

[1] Conservation unnecessary.

canna, a cane or reed, applied to the bark which assumed the form of a roll or quill in drying, the name given by Browne to the West Indian plant "the *Canella alba* of the shops.") — WILD CINNAMON, CINNAMON-BARK.

Probably a single species wide-ranging in the West Indies and with outlying stations in northern South America and in the region of Cape Sable and the Florida Keys, in subtropical Florida, where the plant occurs in hammocks with other tropical genera, generally in the shade of larger trees.

Oil cells are conspicuous in most parts of the plant and the pale inner bark has a cinnamon-like odor. It has been used as a spice, stimulant and tonic. The wood is hard and very dense. The maroon flowers, glaucous on the outside, are borne primarily in June and July (January?) and the crimson fruit matures from March to April. The ripe fruit is eaten by birds which probably disperse the plant. It is cultivated as an ornamental to a limited degree.

The stamens are so closely united that the 10 anthers appear to be a ring of 20 close-packed anther-sacs, each splitting longitudinally. However, ten vascular bundles are present in the tube composed of the filaments.

The genus stands apart in the family by the 10 stamens and the 5 petals coherent only at the base.

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CALYCANTHACEAE (CALYCANTHUS FAMILY)

Shrubs with opposite, entire, exstipulate leaves, numerous strap-shaped tepals spirally arranged on a cup-shaped receptacle, the stamens at its apex and extrorse and the carpels numerous, free, on the inner surface of the receptacle, the mature receptacle resembling a large, dry rose-hip; embryo large, the cotyledons convolute, endosperm lacking.

A small family of disjunct distribution including only two very similar genera (sometimes combined): *Calycanthus* L. (about 4 species of the eastern and western U. S.) and *Chimonanthus* Lindl. (2 or 3 species of China).

The group is notable not only for its odd floral structure (highly modified receptacle and numerous free tepals, stamens and carpels) but for a number of anatomical features, including ethereal oil cells, dicolpate pollen (a modification of the monocolpate type), unilacunar nodes with a fundamentally double trace from a single gap, and 4 cortical vascular bundles (with inverted orientation of xylem and phloem) which extend throughout the stems of mature plants and which have branches entering the leaves at the nodes.

Although some authors have placed the family in the Rosales, the total evidence available clearly indicates that its relationships are with the Ranales, especially that group of families characterized by monocolpate and derived types of pollen and double-trace unilacunar nodes (or unilacunar modifications): Austrobaileyaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Chloranthaceae, and Lactoridaceae. Its closest relationships are probably with the Monimiaceae, a tropical group, chiefly of the southern hemisphere.

1. **Calycanthus** L. Syst. Nat. ed. 10. 2: 1066. 1759, nom. cons.

Deciduous shrubs with opposite, entire, exstipulate leaves and red-brown, purple-brown or greenish solitary flowers terminal on short, leafy axillary branches of the season. Receptacle cup-shaped, bearing on its outer surface and apex bracts and numerous undifferentiated strap-shaped, free, rather fleshy tepals. Stamens numerous, on the edge of the receptacle, with stout filaments, the apex of the connective prolonged, succulent, the anthers extrorse; inner stamens reduced to staminodia; pollen 2-colpate. Gynoecium of numerous free carpels within the receptacle; style filiform, stigma terminal, the ovary 1-celled with 2 anatropous, 2-integumented ovules. Fruit an indehiscent pseudocarp from the accrescent receptacle and tepal-bases, somewhat resembling a large dry rose-hip, bearing within it the numerous large achenes with tough exocarp. Seed solitary, large, lacking endosperm, the embryo large, with convolute cotyledons. $2n = 22$. (*Butneria* Duham., 1755, nom. rejic.) TYPE SPECIES: *C. floridus* L. (The name from Greek, *calyx*, a cup, and *anthos*, flower.) — STRAWBERRY BUSH, SWEET-SHRUB, BUBBY BLOSSOM, SWEET BUBBY, SWEET BETTIE, SPICEBUSH.

Perhaps three species of the eastern United States and a single well marked, less closely related species, *C. occidentalis* Hook. & Arn., of the North Coast Ranges and Sierra Nevada foothills of California. The 2 or 3 species of the Asiatic *Chimonanthus*, in which the number of stamens is reduced to five, are sometimes included in *Calycanthus* as a separate section. *Calycanthus fertilis* Walt., *C. floridus* L., and *C. Mohrii* (Small) Pollard are generally recognized in our area, but the range of variation and the true limits of the species are not well understood. Fruit characteristics have been little used but may provide good taxonomic characters.

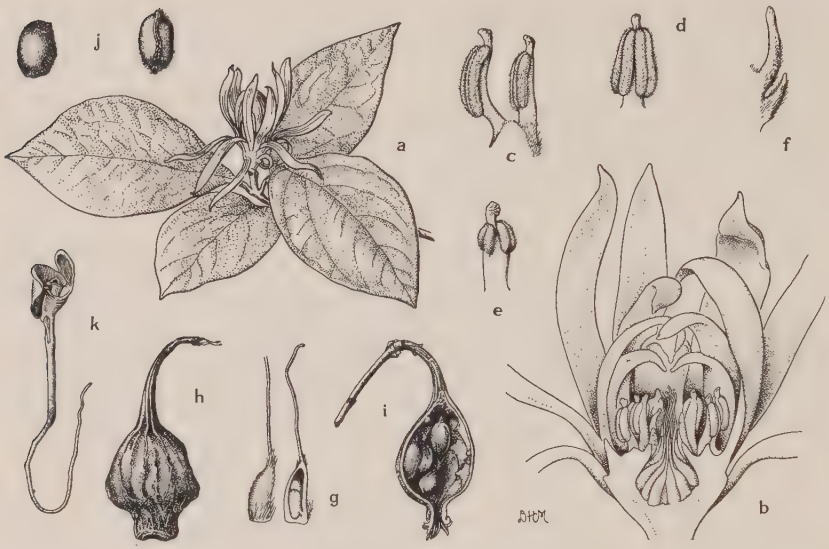

FIG. 3. **Calycanthus.** a–h, *C. floridus*: a, flowering branchlet, × 1/2; b, flower, vertical section, to show carpels, stamens, staminodia, and cup-shaped "receptacle," × 2; c, two stamens, lateral view, × 5; d, stamen, abaxial view, × 5; e, inner, reduced stamen, abaxial view, × 5; f, two staminodia from edge of cup, lateral view, × 5; g, carpels, × 5; h, mature dry pendulous pseudocarp, × 1/2; b, g, semi-diagrammatic. i–k, *C. fertilis*: i, pseudocarp, vertical section, with mature carpels, some removed, × 1/2; j, mature carpels, lateral and abaxial views, × 1; k, seedling with unfurling cotyledons, × 1/2.

Agamospermy (which may account for some of the taxonomic difficulties) has been reported in *Calycanthus fertilis*, *C. floridus*, *C. occidentalis* and *Chimonanthus praecox*. Embryos seem to be of nucellar origin, although parthenogenesis has been claimed for the same species. Pseudogamy appears to be the rule, pollination being necessary for the development of the endosperm, without which the embryo does not grow. *Calycanthus floridus* var. *ovatus* (Ait.) DC., presumably of garden origin, has been reported to be a triploid ($2n = 33$), with about 50 per cent sterile pollen.

The flowers are proterogynous. Pollination in *Calycanthus occidentalis* has been shown to occur through the agency of *Colopterus truncatus* (Randall), a small nitidulid beetle.

Ethereal oil cells occur especially in bark, leaves, and tepals. The flowers are quite variable in fragrance but some forms have an extremely pleasant spicy, strawberry-like odor when crushed. The seeds contain an alkaloid, calycanthine, with a physiological action similar to strychnine; poisoning of cattle and sheep eating the fruits has been reported in Tennessee.

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LAURACEAE (LAUREL FAMILY)

Evergreen (mostly) or deciduous trees or shrubs with alternate [or sometimes opposite or subopposite], exstipulate, entire or rarely lobed, pinnately veined, subtripli-veined [tripli-veined or 3-veined] leaves, (except *Cassytha*, a greatly reduced parasite resembling *Cuscuta*); wood and leaves usually with ethereal oil cells and often with mucilage cells. Inflorescences usually axillary, basically cymose, paniculate or reduced and sub-umbellate, racemose, spicate [or capitate]. Flowers bisexual or unisexual (the plants then dioecious or polygamo-dioecious), small, regular, generally whitish or yellowish, often hairy. Perianth regular, of 6 tepals in 2 whorls of 3, similar or the outer smaller, free nearly to the base or ± united to form a perianth tube on which the stamens are inserted. Stamens basically 12, in 4 series of 3, the outermost (series I) opposite the outer whorl of tepals, the succeeding series alternating; any one or more series (in all our genera) reduced to staminodia or altogether lacking and the filaments of one (series III) or more series of fertile stamens flanked by stalked or sessile "glands." Anthers 4- or 2-locular, introrse or extrorse, upwardly dehiscent by 4 or 2 flap-like valves; pollen sticky, the contents of each locule raised upward by the valve, grains non-aperturate, single. Pistil 1, with a single stigma and style and a 1-locular ovary with a single pendulous, anatropous, 2-integumented ovule; ovary free from the perianth tube, although sometimes ± surrounded by it. Fruit a berry or drupe; perianth lobes persistent [often accrescent] or deciduous in fruit, the perianth tube and pedicel often greatly enlarged to form a cupule subtending the fruit, in a few (e.g., *Cassytha*) the perianth tube completely surrounding the fruit but free from it. Seed lacking endosperm, the embryo large with fleshy plano-convex cotyledons, a small plumule and radicle; germination usually hypogeal. (Including Cassythaceae.)

A family of perhaps 30–40 genera and about 2500 species, mostly evergreen and primarily of the tropics and warm-temperate areas of both hemispheres, especially Central and South America and southern Asia. Represented with us by about 11 native and 2 more or less naturalized species in 8 genera.

The family is easily recognized by the small, regular, usually 3-merous flowers with their curious 4- or 2-locular stamens dehiscent by as many flap-like valves, the 1-locular ovary with a single pendulous anatropous ovule, the baccate fruit often subtended by a cupule derived from the accrescent perianth tube, and the large embryo without endosperm. Equally well characterized by a unique combination of anatomical characters, the Lauraceae seem to form a well-marked and natural family.

The relationships of the Lauraceae seem to be with that group of the woody Ranales (sensu lato) which have secretory cells, unilacunar nodes

and monocolpate, dicolpate or derived (in this case non-aperturate) pollen grains. The relationships are particularly with Monimiaceae (cf. subfam. Hortonoideae, Atherospermoideae), Hernandiaceae, and Gomortegaceae (note woody habit, non-aperturate pollen grains, stamens with associated staminodes, valvular anthers, unilacunar nodes, simple and exstipulate leaves, related alkaloids).

Although the family is a natural one, the generic (and specific) lines are very difficult in some groups of Lauraceae and may be artificial in many instances. Convergent tendencies may be noted again and again. Strong emphasis has been placed upon the various permutations and combinations possible within the 4 series of stamens and staminodes and upon the 4- vs. 2-locular condition of the anthers (although both of the latter are known to occur within some undoubtedly related groups, e.g., *Cinnamomum*, *Sassafras*). Other important characteristics include inflorescence-type and the development of the perianth tube and lobes and their condition in fruit (persistent, deciduous, cupules, etc.). Patterns of leaf-venation and cuticle may be useful at the specific level but may vary widely within related groups and similar patterns may occur in completely unrelated species. (As a result, generic determinations of fossil materials based on vegetative characteristics are, at best, dubious.)

The four trimerous whorls of stamens in the basic lauraceous flower are designated here as series I–IV (cf. Mez), beginning with the outermost whorl which is opposite the outer tepals. The stamens of series III are usually flanked by nectaries (most often stalked and vascularized) which seem to be staminodial in origin. Series IV, if present at all, is usually staminodial.

Perfect flowers throughout the family probably are proterogynous, although observations from living plants seem to have been made only on two species of *Persea*, in which proterogyny is carried to an extreme (dianthesis). Stamens appear to elongate between the time the stigma is receptive and that at which the pollen is shed. The anther valves open from the base upward, recurving and carrying with them the entire contents of the locules.

Only a few species have been examined cytologically, but in these 12 is the basic chromosome number.

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Key to the Genera of Lauraceae

A. Foliose trees and shrubs; not parasitic. Subfam. Lauroideae.
  B. Plants evergreen; inflorescences variously cymose-paniculate, with no involucre at the base; flowers bisexual; anthers of at least one series of stamens (III) extrorse. Tribe Perseeae.
    C. Anthers 4-loculed; fertile stamens 9, the 2 outer series introrse; fruits without cupules or the cupules without evident double margins.
      D. Staminodia of series IV large, cordate-stipitate; locules of anthers of 2 outer series in 2 planes, one above the other.
        E. Fruit without a cupule at the base, the not greatly enlarged perianth persistent (or sometimes completely deciduous); leaves pinnately veined, lacking glands in the axils of the main veins beneath; perianth lobes unequal to subequal. . . 1. *Persea.*
        E. Fruit with a shallow cupule at the base, the perianth lobes deciduous from the enlarged tube; leaves pinnately or subtriplicveined, with conspicuous glands in the axils of the main veins beneath; perianth lobes equal. . . . . 2. *Cinnamomum.*
      D. Staminodia of series IV small, inconspicuous, stipiform; locules of anthers of 2 outer series arranged in an arc. . . . . 3. *Nectandra.*
    C. Anthers 2-loculed; fertile stamens only 3, extrorse; fruits subtended by thick cupules with evident double margins. . . . . 4. *Licaria.*
  B. Plants deciduous, the small yellow flowers produced before or with the unfolding leaves; inflorescences racemose or sub-umbellate in the axils of enlarged bud-scales (*Sassafras*) or with an evident involucre of scales at the base; flowers usually unisexual; fertile stamens 9, the anthers of all series introrse. Tribe Litseeae.
    F. Inflorescences racemose, at the tips of branches, subtended by the enlarged, involucre-like bud-scales; leaves unlobed or with 2 or 3 lobes; fruit a dark blue drupe on a swollen red cupule; anthers 4-loculed; shrubs or trees. . . . . 5. *Sassafras.*
    F. Inflorescences sub-umbellate, involucrate with 4 or 5 decussate scales; fruits bright red on unswollen or slightly swollen pedicels; shrubs.
      G. Anthers 2-loculed; inflorescences nearly sessile; branchlets not evidently zig-zag. . . . . 6. *Lindera*
      G. Anthers 4-loculed; inflorescences clearly pedicellate; branchlets zig-zag. . . . . 7. *Litsea.*
A. Parasitic orange to green twining herbs of tropical Florida; leaves reduced to scales; anthers 2-loculed; fruit surrounded by the persistent fleshy perianth tube. Subfam. Cassythoideae. . . . . 8. *Cassytha.*

Subfam. LAUROIDEAE Kosterm.

Tribe PERSEEAE Mez

1. **Persea** Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.[1]

Evergreen trees and shrubs with chartaceous to coriaceous pinnately veined (usually more or less pubescent) leaves. Inflorescences axillary, peduncled, cymose or rarely sub-umbellate (usually described as paniculate but in ours small, with the exception of *P. americana*). Flowers bisexual, small. Perianth lobes 6, free nearly to the base, the 3 outer ones usually shorter than the inner ones, hairy and persistent in fruit. Fertile stamens 9, staminodia 3; stamen filaments slender, hairy, the anthers 4-loculed, the bases of the 2 upper locules laterally tangential to the apices of the 2 lower; stamens of series I & II introrse; stamens of series III extrorse (or the 2 upper locules lateral and the lower extrorse), the filaments flanked by 2 glands near the base; series IV sterile, the staminodia stipitate with cordate-sagittate tips. Ovary subglobose, the style slender, usually pubescent. Fruit baccate, small and globose or [in *P. americana* and relatives] large and fleshy and obovoid to pyriform (often obliquely so), borne on the spreading perianth-lobes and scarcely enlarged pedicel; [perianth lobes occasionally deciduous in fruit in some forms of *P. americana*]. (*Farnesia* Heist., 1763, nom. rejic.; incl. *Tamala* Raf.) TYPE SPECIES: *Laurus Persea* L. = *P. americana* Miller. (The name an ancient one used by Theophrastus, transferred by Plumier to one of the tropical American species of *Nectandra* and afterward adopted by Linnaeus.)

As usually delimited, a genus primarily of tropical America but reaching south to Chile and northward in our area to Delaware and Arkansas and with a single species *P. indica* (L.) Spreng., in the Canary Islands. Two or three native species occur in our area; *P. americana*, in general cultivation throughout tropical America and an important crop in southern Florida, persists after cultivation and has escaped to hammocks. Kostermans has extended the limits of *Persea* to include a number of Asiatic genera.

Persea Borbonia (L.) Spreng., the red bay, is a handsome tree of the borders of streams and swamps and "bayheads," ranging from Florida to Texas, northward to southern Arkansas and Delaware. A variant, *Persea palustris* (Raf.) Sarg., distinguished primarily on the basis of pubescence is currently treated as f. *pubescens* (Pursh) Fern. ($2n = 24$). A third plant, *P. littoralis* Small, of coastal dunes of Florida, is a small tree with small leaves mostly obtuse at the apex and smooth beneath. The variation in this group is in need of further study. *Persea humilis* Nash, scrub bay, is a distinctive shrub or small tree of the *Pinus clausa–Ceratiola* "scrub" of central Florida. Its habit and habitat, reduced inflorescences, somewhat larger fruits, and small leaves silky with shining golden hairs beneath, are characteristic.

[1] Conservation unnecessary.

The avocado, *Persea americana* ($2n = 24$) introduced into Florida at an early date by the Spaniards and long casually cultivated there, has become an increasingly important fruit crop in southern Florida in the last 40 years. Commercial plantations are concentrated especially in Dade County (about 4/5 of the total crop) but extend about as far north as Cape Canaveral, on the east coast, and Tampa, on the west. Scattered trees of the hardier cultivars may be found considerably farther north, however. A large technical and horticultural literature including much of the information available on the genus has accumulated in connection with the cultivation of this species.

Persea americana is a complex species of very wide distribution in cultivation in tropical America. Its origin presumably lies in Central America and involves the group composed of *P. americana,* its var. *drymifolia* (Schlecht. & Cham.) Blake, *P. Schiedeana* Nees, *P. floccosa* Mez, *P. nubigena* L. O. Williams, and others, all of the uplands of this region. At the present time three general groups of cultivars are recognized: West Indian (originally introduced there from Central America by the Spaniards), Guatemalan, and Mexican. The three groups differ in characters of foliage, fruit, time of flowering and ripening of fruits, and hardiness. *Persea americana* var. *drymifolia,* of the Mexican uplands, is most intimately involved in the Mexican cultivars which are the important commercial types in California but which are not well adapted to the conditions of tropical Florida, where Guatemalan and West Indian forms grow best. In recent years hybrids between members of the three groups have been made and some of these are quite successful (e.g., the 'Booth' cultivars, 'Hickson,' and 'Lula').

The flowers of avocados are proterogynous and have two periods of opening on successive days (dianthesis), the flowers closing in between. "A" and "B" types are recognized. In the former the stigmas are receptive in the morning; the flowers close by early afternoon to re-open the following afternoon when the pollen is shed. In type "B" cultivars, the first (pistillate) opening occurs in the afternoon and the second the following morning. All of the flowers open on a tree at a given time will be in the same stage: thus self-pollination is virtually impossible and both "A" and "B" cultivars are necessary for cross-pollination, an important consideration in the planting of commercial groves. In a sub-type of the "B" form the first period opening is mostly suppressed, with only a few flowers open in the afternoon and most having only a single fairly long period of opening in the morning when the stigmas appear to be receptive and the pollen is shed. Such trees set very few fruit. Beyond this species, observations on pollination appear to have been made only on *P. Skutchii* C. Allen, of Costa Rica and Panama, which also shows dianthesis with equal numbers of "A" and "B" plants but with the two periods of anthesis between dawn and late-morning (10–11 A.M.) and late-morning and early afternoon (2–3 P.M.) on successive days.[2]

[2] Since the above was written, it has been possible through the kind hospitality of Mr. and Mrs. George R. Cooley for Dr. K. A. Wilson and the author to make some

Persea is generally considered to be most closely related to *Phoebe* Nees, a large genus of the tropics of both hemispheres. These genera are conventionally differentiated on the basis of position of anther-locules and nature of the perianth in fruit. Kostermans would reject the former as a generic criterion and would restrict Asiatic *Phoebe* to those species with an appressed and indurated perianth. The New World species might be retained partly in *Phoebe* or assigned to *Persea* and perhaps *Cinnamomum*. The same author greatly extends the limits of *Persea* to include the Asiatic genera *Machilus* Nees, *Nothaphoebe* Blume, *Alseodaphne* Nees, *Stemmatodaphne* Gamble, and *Caryodaphnopsis* Airy-Shaw, the first three of which would be retained as subgenera.

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FERNALD, M. L. Botanical specialties of the Seward Forest and adjacent areas

preliminary observations on dianthesis in *Persea Borbonia* and f. *pubescens* near Brooksville, Hernando County, Florida. Four plants (one the glabrous form and three the pubescent) which began to flower in late April were observed on several days then and in early May 1958. As in *Persea americana* and *P. Skutchii*, dianthesis occurred, with both "A" and "B" types being represented (two of each), but, in contrast to these species, the two periods of anthesis occur in the afternoon. Each of the four plants held to a slightly different schedule, but the first afternoon period commenced about noon and ended between 3 and 4:30 P.M. (Eastern Standard Time). The other period of opening occurred between about 3:30 and 4:45, these flowers remaining open until dark (about 7:30) or after, but those of three plants closing before 8 and those of the fourth before 8:30. Flowers in the staminate (second) anthesis are noticeably less rapid in their final closing response, and a few on "B" plants may overlap the opening of new flowers in the pistillate (first) anthesis. Several large wasps and flies were observed visiting the flowers, along with minute flies, small beetles and ants, all apparently collecting nectar. Plants of *Persea humilis* seen at 3 P.M. in Highlands County, Florida, on May 4, 1958, showed only closed flowers, but branches of one of these (of the "B" type) placed in a polyethylene bag showed later that afternoon and the following day periods of anthesis which appeared to correspond roughly to those of *P. Borbonia*.

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2. **Cinnamomum** Trew, Herb. Blackwell. Cent. 4, signature M. *t. 354*. 1760; Blume, Bijdr. Fl. Nederl. Indië 568. 1825 [1826].

Evergreen trees with [or without] conspicuous buds with imbricate scales, the alternate [or opposite] leaves pinnately veined, subtripli-veined, [tripli-veined, or 3-veined], with [or without] glands in the axils of the veins beneath. Inflorescences paniculate, axillary, with deciduous bracts, produced on the growth of the season. Flowers small, inconspicuous, bisexual [rarely polygamous]. Tepals equal, [persistent or] deciduous from the perianth tube. Fertile stamens 9, the anthers 4 [rarely 2]-loculed; staminodia 3: stamens of series I & II introrse, glandless; stamens of series III flanked by glands at the base of the filament, the anthers [extrorse or] the 2 upper locules laterally extrorse, the lower extrorse; series IV of conspicuous stipitate cordate-tipped glandless staminodes. Stigma discoid or peltate. Perianth tube accrescent in fruit, growing out into a thin cup surrounding the base of the fruit; perianth lobes deciduous from the tube

[or the basal part of the entire lobes persistent on the rim]. Fruit in ours a black, globose drupe. (Including *Camphora* Trew, loc. cit. signature L. *t. 347*; Nees in Wall. Pl. As. Rar. 2: 61, 72. 1831.) TYPE SPECIES: *Laurus Cinnamomum* L. = *C. zeylanicum* [Garc.] Blume. (The name the Latin transcription of Greek *kinnamomon*, derived, in turn, through Hebrew from the ancient name for cinnamon.) — CINNAMON.

A large genus (100–275 species) of eastern Asia, with the largest number in India, Indo-China, China, and Japan, but also in the Philippines, Indonesia, New Guinea, Polynesia and Australia. No species are currently recognized from the western hemisphere, although Kostermans has suggested that some of the American species currently assigned to *Phoebe* Nees may well belong to *Cinnamomum*.

Section CAMPHORA (Trew) Meissn., characterized by completely deciduous perianth lobes, conspicuous perulate vegetative buds, and alternate leaves with pinnate venation (rarely 3-veined or tripli-veined) and with glands in the axils of the veins, is represented with us by *C. Camphora* (L.) Nees and Ebermaier ($2n = 24$). The wood of this species, native to the warm-temperate and subtropical rain-forest zone of eastern Asia from southern Japan to northern Indo-China but now widely planted in the tropics throughout the world, is the source of camphor, which is removed by distillation. The plant was introduced into Florida as early as 1875 as a shade tree and was later established in large plantations in a not very successful attempt to promote a camphor industry in competition with that of Formosa and Japan. At the present time this handsome evergreen with conspicuous scaly buds, very small glaucous flowers (March–April) and black, globose drupes is cultivated in our area as an ornamental tree and for windbreaks from southern Georgia and Florida to southern Louisiana (also s. Texas and Calif.). It is hardy wherever the temperature does not fall below 15°F and has become naturalized to varying degrees throughout this region.

Section CINNAMOMUM (*Malabathrum* Meissn.), in which the perianth lobes are persistent or abscis above the base (leaving the tube crowned by the truncate lobes), the leaf-buds naked or with obsolete scales, and the leaves opposite or subopposite, 3- or tripli-veined and without glands, occurs only in cultivation in the warmer parts of Florida. *Cinnamomum zeylanicum* ($2n = 24$), the cinnamon of commerce, is a tender plant in sub-tropical Florida, while *C. Cassia* Blume, of China, is a more hardy species in that area.

The flowers of *Cinnamomum* are similar to those of *Persea* and *Phoebe* but the perianth tube usually is deeper and grows out to form a thin cup in which the fruit sits. Some species have the anther-locules arranged in an arc (*Neocinnamomum* Liou), a situation paralleled in *Phoebe* vs. *Persea* and *Nectandra* vs. *Ocotea*. Close relationships with *Aiouea* Aubl. and *Phoebe* and also with *Ocotea* have been postulated by Kostermans.

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3. **Nectandra** Rolander ex Rottböll, Acta Lit. Univ. Hafn. 1: 279. 1778, nom. cons.

Trees [and shrubs] with alternate coriaceous [to membranaceous] leaves usually pinnately veined, the reticulation conspicuous [or obscure].

Inflorescences usually paniculate, axillary or subterminal, the narrow bracts deciduous. Flowers bisexual, small, the 6 elliptic perianth lobes hairy, spreading or reflexed at anthesis, deciduous, the tube conspicuous or almost entirely lacking. Fertile stamens 9, the staminodia 3 [when present]: stamens of 2 outer series (I & II) with nearly sessile reniform anthers [or fleshy and petaloid], the anther-locules 4, arranged in an arc, introrse. Stamens of series III longer, the squarish anthers on filaments almost equal their length, with 2 large subreniform nearly sessile glands at the base of filaments, the 4 anther-locules in two horizontal planes, the 2 upper laterally extrorse, the 2 lower extrorse. Staminodia stipiform (in ours triquetrous, on slender pubescent filaments). Ovary glabrous; stigma capitate, conspicuous. Fruit a thin-walled drupe, ellipsoid, globose or oblong, with a shallow woody cupule (formed by the enlarged perianth tube) subtended by the enlarged pedicel; cupule margin simple. (Not *Nectandra* Berg., 1767.) TYPE SPECIES: *N. sanguinea* Rol. ex Rottb. (The name from Greek, *nektar*, nectar, and *andros*, of a man, in reference to the stamens and anther valves which were mistaken for nectaries and stamens, respectively.) — LANCEWOOD.

A large genus (about 175 sp.) of tropical America, the majority of the species in South America (especially the Andes), with about 35 in Central America, and a few in the West Indies. *Nectandra coriacea* (Sw.) Griseb. (*Ocotea coriacea* (Sw.) Britton), which occurs in the West Indies, the Yucatan Peninsula, British Honduras, and Guatemala, reaches southern Florida, where it extends as far north as Indian River County, on the east coast, and Cape Romano (Collier County), on the west.

This species, which may reach 30–40 feet in height, bears small panicles of small, white, very fragrant jasmine-scented flowers which are followed by the first green, then dark-blue, then black fruit with green, yellow or red cupule and enlarged fruiting pedicel. Flowering and fruiting are quite variable. The leaf-venation is its most outstanding characteristic: there are 6–8 pairs of lateral nerves which are rather obscured by a very conspicuous over-all elevated reticulum (at least in dried specimens). *Nectandra coriacea* is most closely related to *N. salicifolia* (HBK.) Nees (*N. sanguinea* sensu Nees, non Bol. ex Rottb.), of wide distribution in Mexico and Central America.

Nectandra is distinguished from *Ocotea* Aubl. (1775) by the arrangement of the anther-locules of the two outer series of stamens, these being in an arc in the former and in two planes in the latter, a distinction which does not entirely hold. Further studies in tropical America may well show that *Nectandra* should be regarded as a subgenus of *Ocotea*, a course recently advocated by Kostermans.

It has been suggested, on the basis of the illustration of *Ocotea Catesbyana* in Sargent, Silva 7: *pl. 303,* that both *Nectandra* and *Ocotea* occur in southern Florida. Although this illustration does show the anther-locule arrangement of *Ocotea*, rather than that of *Nectandra*, this would appear to be an error, for only *Nectandra coriacea* (also incorrectly drawn

in Small's Manual) seems to be represented by herbarium specimens, including those studied by Sargent, from southern Florida. The disposition of *Ocotea Catesbyana* (at least *sensu* Sargent) as a synonym of *N. coriacea* would appear to be the correct one.

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SARGENT, C. S. *Ocotea.* Silva N. Am. **7:** 9–12. *pl. 303.* 1905. [*N. coriacea,* as *O. Catesbyana*; details of stamens incorrect.]

4. **Licaria** Aubl. Hist. Pl. Guiane Franç. **1:** 313. *pl. 121.* 1775.

Evergreen trees [or shrubs] with pinnately-veined leaves and small flowers in axillary or subterminal panicles near the tips of the branchlets [or flowers rarely solitary, subumbellate or capitate]. Flowers bisexual; tepals 6, in two whorls, [spreading or] erect, united below into a distinct perianth tube; (in ours, flowers obconical, ca. 2–2.5 mm. long, the perianth tube about half this length). Fertile stamens 3: stamens of series I & II [small and staminodial or] abortive; stamens of series III fertile, [entirely free, partly connate or] united into a staminal tube, their anthers 2-loculed, extrorse [or introrse], the filaments each with 2 glands (these in ours flattish, pressed against the staminal tube below the anthers, united in pairs, touching each other); stamens of series IV abortive [or rarely staminodial, minute]. Ovary included in perianth tube, free, the style thick [to slender], stigma inconspicuous. Berry ellipsoid, (in ours black, to 2 cm. long), smooth, the base partly covered by a thick, hemispherical double-margined cupule, the inner margin entire, erect, the outer one spreading, thicker, irregular, the pedicel thickened, merging into the tube. Cotyledons flat-convex, large, including the minute 2–4-leaved, glabrous plumule and minute conical radicle. (*Acrodiclidium* Nees & Mart. 1833; incl. *Misanteca* Schlecht. & Cham. 1831, *Chanekia* Lundell, 1937 and others.) TYPE SPECIES: *L. guianensis* Aubl. (The name derived from *licari kanali,* the native name of the type species.) — SWEETWOOD.

A genus of about 45 species of wide distribution in tropical South and Central America and the West Indies; a single species, *L. triandra,* of the West Indies from Martinque to Cuba, has been known from a single locality in our area.

The handsome *Licaria triandra* (Sw.) Kostermans (*Misanteca triandra* (Sw.) Mez) is one of the rarest plants in our flora, if it still persists at all. It was first recorded from two trees discovered in 1910 in Brickell Hammock, in Miami, but as many as 25 trees were counted there as recently as 1946 by the late W. M. Buswell (see Little, Checklist of Native and Naturalized Trees of U. S.). However, this unique hammock has been swallowed up and destroyed by the greedy real-estate development of metropolitan Miami and the species is presumably extinct at that locality. Apparently a few trees (planted) still survive on the campus of the University of Miami.

Licaria, as used here, includes, among others, *Acrodiclidium* (characterized by the presence of series I and II as staminodes, the stamens of series III free), *Misanteca* (in which staminodia are lacking and the stamens of series III united), and *Chanekia* (lacking staminodia and with stamens free). These genera merge with one another and share their "general facies, the shape of the cupule, ovary and stigma," characters which also separate them from *Mezilaurus* and *Endiandra,* their nearest allies (Kostermans).

Although there is agreement that the group as now constituted is a natural one, the proper name for it has been a matter of dispute. *Licaria* is based upon sterile material which Kostermans identifies positively with *Acrodiclidium*; Lundell, however, rejects *Licaria* in favor of *Misanteca* because the genus is based upon a sterile specimen.

Our species falls into subgenus Misanteca (Schlecht. & Cham.) Kostermans. Apparently *L. triandra* [West Indies], *L. limbosa* (Ruiz & Pavon) Kosterm. [Venezuela to Peru and Bolivia], *L. Pittieri* (Mez) C. Allen [Costa Rica], *L. Cervantesii* (HBK) Kosterm. [southern Mexico, Guatemala], *L. caudata* (Lundell) Kosterm. [Br. Honduras, Guatemala], and *L. Cufodontisii* Kosterm. [Costa Rica] form a group of more or less closely related species.

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Tribe Litseeae Mez

5. **Sassafras** Trew, Herb. Blackwell. Cent. 3, signature p. *t. 267*. 1757; T. F. L. Nees & Ebermaier, Handb. Med.-Pharm. Bot. **2:** 418. 1831.

Deciduous trees with elliptic leaves, entire, mitten-shaped or 3-lobed at the apex, narrowed at the base, involute in the bud; buds with few imbricate outer scales. Plants usually dioecious, the flowers usually unisexual [or apparently bisexual, but not often functionally so], in lax, drooping, few-flowered "racemes," the upper flowers of the lowest raceme opening first. Perianth of 6 yellowish tepals, in two whorls of 3. Staminate flowers with 9 fertile stamens on the margin of the short perianth tube; anthers 4[or 2]-loculed, introrse (but the lower locules of series III latrorse), opening by 4[or 2] valves; filaments flattened, elongated, those of series III with a pair of orange-colored short-stipitate glands at the base; staminodes and pistillode absent [or 3 staminodes and pistillode present in the Asiatic species]. Pistillate flowers with 6 rudimentary stamens, in 2 whorls [or 12 in 4 whorls, similar to stamens and staminodes in staminate flowers]; ovary ovoid, nearly sessile in the short perianth tube, the style slender, the stigma enlarged. Fruit a dark blue ovoid berry supported by the club-shaped enlarged and fleshy pedicel and perianth base. Seed oblong, pointed; testa thin; embryo subglobose, erect. (Including *Pseudosassafras* Lec., *Yushunia* Kamikoti.) TYPE SPECIES: *Laurus Sassafras* L. = *S. albidum* (Nutt.) C. G. Nees. (The popular name for the plant, used as early as 1569 by the French in Florida, adopted by Trew.)

As currently delimited, a genus of three species of eastern American-eastern Asiatic distribution: *Sassafras albidum* ($2n = 48$) (including var. *albidum* and the more southern var. *molle* (Raf.) Fern.), of wide distribution from s. Maine to se. Iowa, s. to Texas and Florida; *S. Tzumu* (Hemsl.) Hemsl., of central China (from Kwantung and Kweichow, to Szechuan, Hupeh, Anhwei, and Chekiang); and *S. randaiense* (Hayata) Rehd., of the central mountain range of Formosa.

The two Asiatic species constitute the subgenus PSEUDOSASSAFRAS (Lecomte) Keng. Both are less specialized than the American and differ from it in the pubescent tepals, in the presence of 3 staminodes and a pistillode in the staminate flowers, and in having in the pistillate flowers 12 staminodes similar in appearance to the stamens and staminodes of the staminate flower. The anthers of *S. Tzumu* are 4-loculed, those of *S. randaiense* 2-loculed. All three plants are similar, however, in habit, bark, winter buds, leaves, inflorescence and fruit and certainly constitute a natural genus (although each of the three has been assigned to a separate monotypic genus at one time or another). Rehder suggested that the nearest relative of *Sassafras* is *Lindera* (some of the deciduous species of which have lobed leaves very similar to those of *Sassafras*) which differs primarily in its 2-celled anthers and in the "umbellate" inflorescence. Kostermans, however, would ally *Sassafras* with the evergreen *Actinodaphne* Nees, a rather different group, more suggestive of *Litsea*.

Sassafras albidum is with us a very familiar plant, long reputed to have medicinal properties. It is at most a mild, aromatic stimulant. Gumbo filé, a powder used to give flavor and consistency to gumbo soup, owes its

properties to the secretory and mucilage cells of the leaves from which it is prepared.

Although seldom planted, the species is one of our most handsome native plants, attractive at all seasons of the year. The tree occasionally reaches a height of 80–90 feet and a diameter of 6 feet. It is sometimes weedy, for it tends to sucker from the roots. The attractive small, yellow flowers are produced in early spring with the first unfolding of the leaves.

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6. **Lindera** Thunb. Nov. Gen. Pl. 3: 64. 1783; Blume, Mus. Bot. Lugd.-Bat. 1: 323. 1851, nom. cons.

Dioecious or polygamo-dioecious shrubs with entire [or 3-lobed] deciduous [or evergreen] leaves. Flowers small, yellow, short pedicelled, in almost sessile [in ours] umbel-like cymose clusters of 3–6, each cluster subtended by 2 pairs of decussate deciduous bracts, the clusters 1–4 above the axils of the preceding year's leaves on greatly reduced supra-axillary branches terminated by a vegetative bud which grows after anthesis. Tepals glabrous, the two whorls similar, thin, the perianth tube very short or none; perianth deciduous, only a small disc remaining beneath the fruit in ours. Staminate flowers with 9 stamens (series IV completely aborted), the 3 innermost (series III) each with a pair of conspicuous stalked glands at the base; anthers 2-loculate, all introrse; pistillodium present. Pistillate flowers with stamens variously developed, the innermost series usually reduced to filaments with two glands at the base; some staminate flowers sometimes present among the pistillate; ovary and style about equal. Fruit a bright red drupe on the short, hardly or slightly thickened pedicel topped by the disc-like somewhat accrescent perianth base. (*Benzoin* Fabr. 1763, non *Lindera* Adans. 1763, nomina rejicienda.) TYPE SPECIES: *L. umbellata* Thunb. (Named for John Linder, 1676–1723, early Swedish botanist.) — WILD ALLSPICE, SPICEBUSH.

A large genus, of about 100 species, both deciduous and evergreen, primarily of eastern Asia, with only two in the western hemisphere, both occurring in our area. *Lindera Benzoin* (L.) Blume, var. *Benzoin* is widespread along streams and in damp woods from southwestern Maine to southern Michigan and Illinois, south to North Carolina, Kentucky, Missouri and southeastern Kansas. Its var. *pubescens* (Palmer & Steyerm.) Rehd. is more southern in distribution, reaching Florida and Texas. *Lindera melissifolia* (Walt.) Blume is apparently exceedingly rare and local being known from widely scattered localities from Florida to Louisiana, northward to southern Missouri and to eastern North Carolina. The two species are quite distinct, differing in their ecology and in numerous morphological features. (See Steyermark.) Both are known to occur close together but in different habitats in southern Missouri.

Lindera Benzoin is a handsome shrub, worthy of cultivation, although, like most native plants, it is seldom grown. The flowers are among the very earliest to appear in spring. Staminate flowers are somewhat larger than pistillate and frequently occur in clusters of 3 or 4 umbels, in contrast to the less conspicuous pistillate inflorescences which are usually either single or paired. As a result, staminate plants are far more frequent than pistillate in the flowering condition in herbaria. This species and the Asiatic *L. praecox* and *L. glauca* have all been reported to have 24 somatic chromosomes.

Characters of flower and fruit in *Lindera* are very similar to those of *Litsea*, the two genera being distinguished primarily by the 2-loculed (or

very rarely partly 4-loculed) anthers of *Lindera* vs. the 4-loculed anthers of *Litsea*.

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7. **Litsea** Lam. Encyc. Méthod. Bot. **3**: 574. 1791, nom. cons.

Dioecious, [evergreen or] deciduous shrubs with pinnately veined leaves and naked [or imbricate-scaled] buds. Flowers unisexual, in small pedunculate axillary sub-umbellate 3–5 flowered clusters, each with an involucre of 4 or 5 decussate deciduous scales, globose before anthesis; in our species borne singly above the scar of leaves of the preceding year near the tips of the branches, or 2 or 3 on very short axillary branches. Tepals yellow, 6 [or occasionally fewer or lacking], almost completely free [or united into an ovoid or campanulate tube], deciduous after anthesis. Staminate flowers with 9 [or 12] fertile stamens, those of series III [and IV] with 2 stipitate glands at the base; filaments well developed, in ours 2–3 times as long as the ovate emarginate anthers; anthers all 4-locular, all introrse; pistillode lacking [or small]; staminodia none in our species. Pistillate flowers with 9 [or 12] staminodia, those of series I and II usually without glands, those of III [and IV] flanked by 2 glands at the base of the filaments; ovary attenuate into the style, the stigma dilated. Fruit a more or less globular berry seated on a minute disc [or on a shallow cupule or disc on the enlarged pedicel]. (*Malapoenna* Adans. 1763, *Tomex* Thunb. 1783, *Sebifera* Lour. 1790; nomina rejicienda. *Glabraria* sensu Blume, 1851, not L. = *Boschia* Korthals [Bombacaceae]). Type species: *L. chinensis* Lam. = *L. sebifera* Pers. (according to list of nomina conservanda) or = *L. glutinosa* (Lour.) C. B. Robinson (according to Kostermans). (The name presumably from a local name of southern China, *litsé*

de Chine being given as the common name for the type species.) — POND-SPICE.

A large genus of perhaps 400 species, mostly evergreen, and primarily of eastern and southeastern Asia from Japan to the Philippines, India, New Caledonia, tropical and subtropical Australia and New Zealand, with 5 species in North America. Of the American species, 3 are distinctive closely related plants of the eastern Sierra Madre of Mexico; the fourth, *L. glaucescens* HBK. is highly variable and widespread from northwestern Mexico east and south to Costa Rica; the fifth, *L. aestivalis* (L.) Fern. (*L. geniculata* (Walt.) B. & H.), is a rare plant of very spotty distribution on the coastal plain from Florida to Louisiana, north to eastern North Carolina, southeastern Virginia (at least formerly), and Tennessee, occurring around pond-margins and in swamps.

Litsea aestivalis is a shrub to 2 or 3 m. with characteristic zig-zag branchlets and narrowly oblong leaves. The pedunculate and involucrate umbel-like clusters of small yellow flowers are borne in early spring before the appearance of the leaves (this being the only deciduous American species). The bright-red globose fruit is borne in early summer.

Like *Lindera*, presumably a close relative (from which it differs primarily in the 4-loculed anthers), the genus is complex and taxonomically difficult in eastern and southeastern Asia, where the interrelationships of *Litsea*, *Lindera*, *Sassafras*, *Actinodaphne*, *Neolitsea* and others are to be sought.

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Subfam. CASSYTHOIDEAE Kosterm.

8. **Cassytha** L. Sp. Pl. 1: 35. 1753; Gen. Pl. ed. 5. 22. 1754, "*Cassyta*."

Parasitic green to orange twining plants with wiry chlorophyll-bearing stems and minute, spirally arranged scale-like leaves, the plants superficially resembling *Cuscuta* and attached to host plants by small haustoria. Inflorescences indefinite, spicate [or racemose or reduced to heads], the

minute flowers borne singly at irregularly separated nodes, sessile [or pedicellate] in the axil of a minute bract, with 2 similar bracteoles close under the perianth, bisexual. Tepals 6, the outer whorl much smaller and resembling the bracts, united below to form a shallow tube to which the stamens are adnate, later accrescent and inclosing the fruit. Fertile stamens 9, 2-loculed, staminodia 3: stamens of series I sub-petaloid, series I & II introrse, without glands; stamens of series III flanked by nearly sessile glands, the anthers extrorse; series IV of distinct cordate sessile [or stipitate] staminodes. Ovary broadly fusiform, the style indistinct, the stigma capitate. Fruit drupaceous with a hard endocarp, completely inclosed by, but free from the enlarged and succulent cream-colored perianth tube which has a small opening at the apex surrounded by the persistent erect perianth lobes. Seed coat membranous or coriaceous; cotyledons thick, fleshy, often unequal, sometimes more or less consolidated at maturity. TYPE SPECIES: *C. filiformis* L. (The name from Greek, *kasytas* or *kadytas*, dodder [*Cuscuta*].) — WOE-VINE, LOVE-VINE.

A curious genus with perhaps 15–20 species, more or less maritime and mainly Australian but with a few in Africa and a single species, *C. filiformis*, of pantropical distribution and the only species in the Americas. *Cassytha filiformis* occurs in the subtropical portions of our area, primarily in coastal areas as far north as Brevard and Pinellas counties, where it may easily be mistaken at first for *Cuscuta*. It is parasitic on a wide range of herbaceous and woody hosts and can be a destructive pest.

Although *Cassytha* is an obligate parasite, the plant is at least partly autotrophic, for chloroplasts with abundant starch are present in the cortical parenchyma throughout the stem. In addition, numerous stomata (oriented transversely on the stem), an extensive xylem system, and haustoria with many well-developed spiral tracheae running to their ends which curve directly into the wood area of the host, all suggest that the plant is primarily a water-parasite. This habit, the reduction in exposed surface, the extreme development of mucilage in the plant (reminiscent of the cacti), and the profuse development of the plant in the brilliant sunlight of coastal and white-sand scrubs suggest further a special adaptation to a xerophytic type of habitat unfavorable to most Lauraceae.

Seedlings germinate in nearly pure sand and elongate quickly with rather rapid nutating movements which bring about contact with a host plant. The primary root remains rudimentary and only four secondary roots (which lack root-caps) function during the period prior to attachment to the host.

Although the inflorescences of *Cassytha* are described as "indeterminate" racemes or spikes or (in a few species) heads, the "inflorescences" would not seem to be radical departures from the usual determinate, basically cymose inflorescences of other Lauraceae, but would merely reflect the reduction to "simplicity" in this highly modified plant. Each of the solitary axillary flowers with its two minute bracteoles would appear to be the product (by reduction) of an entire cymose lauraceous inflorescence.

Thus the short "racemes" or "spikes" of *Cassytha* would represent a stem with inflorescences (each reduced to one flower) produced at successive nodes, just as in many Lauraceae a succession of axillary inflorescences is produced as the growth of the season proceeds. The even more highly modified capitate inflorescences of some species of *Cassytha* would be derived through shortening of the internodes of "spicate" inflorescence.

Cassytha is sometimes separated from the Lauraceae on account of its great reduction and parasitic habit but in all anatomical features (including rubiaceous stomata, ethereal oil cells and mucilage cells) and in all floral characters it is very clearly a member of that family. In flower and fruit it approaches *Cryptocarya* R. Br., a large pantropical genus, in which the fruit is completely inclosed in the enlarged perianth tube.

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STATISTICS OF COMPOSITAE IN RELATION TO THE FLORA OF CHINA

Shiu-ying Hu

In July 1953 a project for the preparation of a descriptive flora of China was initiated in the Arnold Arboretum under the auspices of the China International Foundation. The first undertaking of the project was the compilation of a comprehensive index to the species of Phanerogams of that country. A staff of five persons spent two and a half years in checking through the extensive botanical literature and in making reference cards of the species of the flowering plants of China. The complete index consists of one hundred and twenty thousand cards, each including name and synonyms of a species, the date and place of publication and the distribution of the taxon as indicated by the citation of various collections, with special emphasis on the type material. This index not only constitutes a comprehensive foundation for the floristic studies and taxonomic researches of the Flora of China Project, but it also reflects a much clearer picture of the vegetation of China than any information we have had before. In a concise and systematic way it tells both the kind of plants which can be found in China and the locations in which each species occurs.

The Compositae constitute the largest family of flowering plants in the world. This statement also holds true for China. The species of Compositae are represented in all parts of the country, from the extensive seashore, in the east, to the alpine tundra of Sinkiang and Tibet, in the west, and from tropical Hainan Island, in the south, to the Mongolian desert, in the north. With the information given on the above-mentioned index cards, I have made an enumeration of the Compositae of China, which gives a total of 219 genera and 3216 species described or recorded from this area. Due to certain nomenclatural changes some of these genera and many of the species have been reduced to synonymy. Meanwhile, because of the treaties made between China and Russia in 1860–64, certain monotypic and oligotypic genera, which were known only from the type localities or from small areas which are no longer within the boundary of China, have to be excluded. Consequently, only 167 genera and 2029 species are here recognized. The basis for choosing the valid binomials has been the recent treatments of various groups by competent taxonomists like Babcock, Chang, Chen, Good, Handel-Mazzetti, Kitamura, Ling, and Stebbins. There is no doubt that the numbers of the recognized taxa will be changed when careful studies of available material are made, the generic limits redefined, and the specific status better determined. Nevertheless, the changes of details probably will not have an appreciable effect on the general picture of the nature, distribution and origin of the vegetation, which an analytic study of the data on the principal elements of the family may reflect.

Up to the present there is no map which shows the phytogeography of China. In recent years students of economic geography as well as of plant geography have tried to prepare phytogeographic maps to illustrate vegetation types in China, but have failed to produce anything which can give a true picture of the vegetation. The difficulty has been that they have not had distributional data of the species that constitute the principal elements of the vegetation. The present paper is an attempt to analyze the distributional data for a large natural group and to utilize it to interpret some of the problems involved in the composition and phylogeny of the vegetation of China. When similar studies on the Gymnospermae, Gramineae, Cyperaceae, Liliaceae, Orchidaceae, Ranunculaceae, Fagaceae, Lauraceae, Rosaceae, Leguminosae and Ericaceae have been made, and with the aid of a few recently monographed families, such as the Magnoliaceae, Theaceae, and Araliaceae, we shall be in a much better position to present a truer phytogeographic map of China.

China is here defined so as to include all the territory covered by W. T. Ting's *Atlas* published in 1934. It has been a general practice among Chinese botanists to include every taxon published from "Manchuria," "Soongoria" and the "Tien-shan Range" in the flora of China. The reason for this practice is that in a standard map of China there is a Manchuria in the northeast (which includes Kirin, Liaoning and Heilungkiang), a Soongaria Basin in western Sinkiang and a Tien-shan in central Sinkiang. But when Maximowicz collected in Manchuria in 1856, and Regel made his Soongaria expedition in 1840 these areas covered much more territory than they do in the present map of China. Due to the 1860 treaty with Russia, the northern and eastern half of Manchuria became a part of the Russian Far East. Likewise, due to the 1864 treaty the western half of Soongaria and western Tien-shan no longer belong to China. For this reason, genera like *Symphyllocarpus* Maxim., from northeastern Manchuria (in the old sense), and *Plagiobasis* Schrenk and *Acanthocephalus* Karelin and Kirilov, from the region of Soongaria beyond the present Chinese border, are excluded from this study.

I. THE TRIBES OF COMPOSITAE

Cassini, in 1812–18, established eleven tribes for the Compositae. Hoffmann in 1889 arranged 806 genera in two subfamilies and thirteen tribes in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* IV. 5: 118. Dalla Torre and Harms in 1905 listed 899 known genera in their *Genera Siphonogamarum*. They placed 877 genera in two subfamilies and thirteen tribes following Hoffman's system and left twenty-two genera as *Genera incertae sedis* at the end. The latest record of the total number of genera of Compositae is found in Lemée's *Dictionaire Descriptif et Synonymique des Genres de Plantes Phanérogames* 7: 484. 1939, where 1014 genera are recognized. In this work the genera of Compositae are dispersed alphabetically among all the genera of the Phanerogams. It is of little use for

our purpose of making comparative studies of the principal elements of the family. For a concise over-all picture of the Compositae and for systematic comparisons of its tribes and genera, the record in Dalla Torre and Harms still appears to be most useful, especially since many of the larger herbaria are arranged according to this scheme. In modern manuals and handbooks such as those of Fernald, Rehder, Bailey, etc., the names of these tribes appear repeatedly. Since both the system and the names are familiar to students of botany, they are adopted in this discussion.

When *Genera Siphonogamarum* was published, the flora of China was little known to the botanical world. It therefore contains rather inadequate information on the Chinese Compositae. The data on the number of genera in each tribe and the distributional notes of the genera as given in this work are here taken unchanged to give a general view of the tribes of the family. To insure clarity the figures on the tribes of Compositae in China as revealed by our studies are given separately.

1. The Tribes of Compositae in General

Dalla Torre and Harm's information on the sizes, ranges and centers of generic concentration of the tribes of Compositae are summarized in the following graph. Abbreviations commonly used in the literature are adopted for the area column with the following exceptions: Med. Reg. = Mediterranean Region; Aust. = Australia; Pac. Is. = Pacific Islands; and Mad. = Madagascar.

With respect to the number of genera most of the tribes are medium-sized, including forty to sixty-five genera. The large tribes are the Astereae, Inuleae and Heliantheae, each of which has over one hundred genera. The small tribes are the Calenduleae and Arctotieae, the former containing 8 genera and the latter 11. The distributional patterns of the tribes are worthy of notice. The small and medium-sized tribes all have definite areas of generic concentration. Even in the large tribes, although they occupy more extensive areas, the centers of the concentration of their genera are evident.

1. The tribe Vernonieae has about 49 genera, 19 of which are from South America, 16 from South Africa, 5 from tropical America, 3 pantropic, 2 in Madagascar, 2 in India, and 1 each in Australia and North America. This distributional record indicates that the Vernonieae is essentially a southern tribe with the centers of concentration in South America and South Africa. Only a few of its genera, such as *Elephantopus* and *Vernonia*, extend to the warm region of the north temperate zone.

2. The tribe Eupatorieae includes about 51 genera, 16 of which occur in South America, 16 in Mexico and Central America, 9 in North America, 3 in the West Indies. A few genera such as *Eupatorium*, *Mikania*, etc., are represented in all warm regions. Thus, this distributional record indicates that the Eupatorieae are essentially a New World tribe with the generic concentration in tropical America.

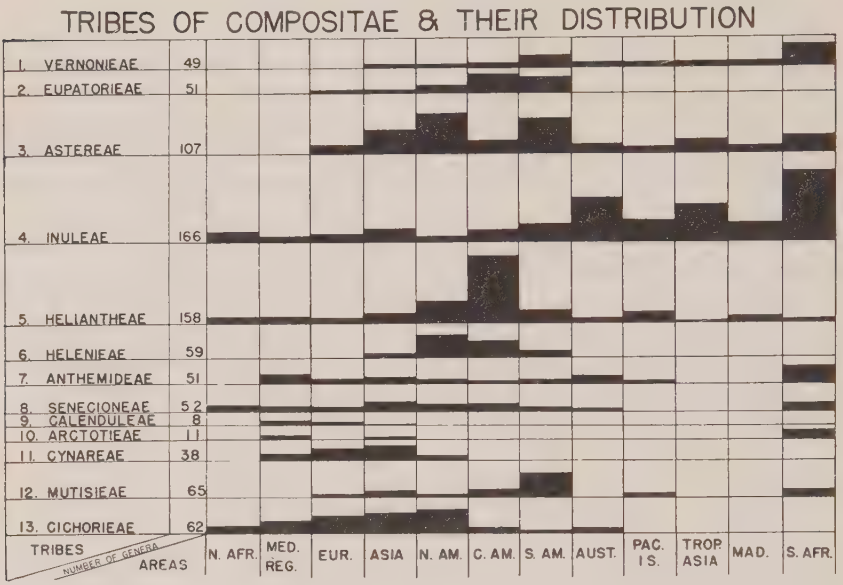

FIG. 1. The tribes of Compositae and their distribution in the world.

3. The tribe ASTEREAE includes about 107 genera, 27 of which are from North America, 19 from South America, 11 from Mexico and tropical America, 18 from Africa, 3 from Madagascar, 2 endemic to St. Helena, 2 in the Hawaiian Islands, 3 in Europe, 5 in Australia and New Zealand, and 4 from Asia. In addition, there are many genera that are widely distributed. For example, *Brachycome* is represented in Australia, Tasmania, New Zealand, eastern and tropical Africa; *Lagenophora* occurs in tropical and eastern Asia, New Zealand, Australia and the Pacific Islands; *Myriactis* is found in New Guinea, Java, India and Central Asia; *Podocoma* is represented in tropical America and Australia; *Vittadinia* occurs in New Guinea, Australia, New Zealand, New Caledonia and South America; and both *Aster* and *Erigeron* have large numbers of species in America, Asia, Europe and tropical Africa. This distributional record clearly indicates that the Astereae encompass both widespread and endemic genera. It has several centers of generic concentration, namely Asia, Africa, and North and South America. It is especially well-represented in the New World.

4. The tribe INULEAE is the largest tribe in the Compositae. Of its approximately 166 genera, 84 are from Africa (especially South Africa), 9 from Madagascar, 37 from Australia, 12 from South America, 4 from tropical America. In addition, 12 are common in the Old World tropics and 4 are pantropical genera. This distributional record indicates that the Inuleae is a southern tribe with the centers of generic concentration in South Africa, Australia and, to a lesser degree, tropical Asia. It is rather poorly represented in the northern temperate regions.

5. The tribe Heliantheae includes about 158 genera, 80 of which are from Central America, 30 from the United States occurring chiefly in the southwestern states from Texas to California, 21 from South America, 6 from the Sandwich Islands, 5 from Madagascar and 3 from Africa. In addition, there are 6 pantropic and 4 cosmopolitan genera. This distributional record clearly indicates that the Heliantheae are a New World tribe and, with the exception of the introduced and adventive elements, one which is poorly represented in the Old World.

6. The tribe Helenieae includes 59 genera, 36 of which occur in the United States and Mexico, 17 in tropical America and 5 in South America. Tropical Africa has two genera, with *Welwitschiella* being endemic. This distributional record indicates that the tribe Helenieae is essentially a New World group. With the exception of the introduced taxa, it is almost absent in the Old World.

7. The tribe Anthemideae includes 51 genera, 18 of which are from South Africa, 10 from the Mediterranean region and the Canary Islands, 4 from Australia, 6 from central and southern Asia, 5 pantropic or cosmopolitan, 1 from North America, 2 from South America and 1 from New Guinea. This record indicates that the Anthemideae are essentially Old World with the generic concentration in South Africa and, to a lesser degree, in the Mediterranean region. The tribe has a few widespread, as well as a few endemic, genera. It is very poorly represented in the New World.

8. The tribe Senecioneae includes 52 genera with 12 occurring in South Africa, 10 in western North America, 4 in Central America, 3 in South America, 2 in the Bourbon Islands, 2 in Australia, 2 in China, 1 endemic to Juan Fernandez Island, and 1 in the European Alps. In addition, three genera are represented in a range covering Africa, Persia and Afghanistan, four in a range covering North Africa, Europe, temperate Asia and North America, two in North Asia, North America, the West Indies and South America, and one, *Senecio*, including 1200 species, occurring throughout the world. At first sight these data do not seem to indicate any significant pattern of distribution for the tribe. But when the Afghanistan-Persia-Africa, the Europe-North Africa-temperate Asia-North America, and the North America-West Indies-South America patterns of distribution are correlated with the continuous chains of high mountains that tie together the continental masses, a very interesting pattern of distribution becomes apparent. Evidently the elements in this tribe are predominantly montane forms. Their distributions correspond with the direction of mountain axes which radiate from western China westward through central Asia to Europe and Africa, northward through northeastern Asia to the Americas and southward through the Malayan Peninsula, the Malayan Archipelago to Australia. The Senecioneae, unlike most other tribes which have obvious centers of generic concentration, are comparatively better represented in eastern Asia, western North America and South Africa.

9. The tribe Calenduleae is the smallest one of the family. It has eight genera, five of which occur in the south of Africa and the rest in the

Mediterranean region and western Asia. The Calenduleae are strictly Old World in distribution.

10. The tribe ARCTOTIEAE is the next smallest tribe in the family. It comprises eleven genera, ten of which occur in South Africa and one from Syria to Persia. It is strictly an Old World tribe.

11. The tribe CYNAREAE has 38 genera, 11 of which are confined to western Asia and Persia, 5 to the Mediterranean region, 12 to a wide range extending from southern Europe through Asia to Japan, 5 to Europe to central Asia, 2 common in the temperate and subtropical regions of the northern hemisphere, 1 endemic to China, 1 to India, and 1 to the Juan Fernandez Islands. The tribe Cynareae is essentially an Old World group.

12. The tribe MUTISIEAE has 65 genera, 36 of which are from South America, 4 from the West Indies, 3 from Central America, 8 from tropical and South Africa, 1 endemic to the Hawaiian Islands, 1 from North America, 1 from the European Alps, 2 to the Himalayan region, 2 to China, 2 to Japan and 1 from Afghanistan to Japan. The Mutisieae are predominantly southern with the centers of generic concentration in South America and, to a lesser degree, in South Africa. In the northern hemisphere the tribe is represented by a few endemic genera and one wide-spread genus.

13. The tribe CICHORIEAE includes 64 genera, of which 16 are confined to North America, especially the western United States, 13 to the Mediterranean region, 2 to Europe, 2 to North Africa, 2 to Australia, 5 to China, 1 to South America, 1 to the Society Islands, and 1 to Juan Fernandez Island. In addition, there are many genera with wide ranges. *Sonchus* and *Taraxacum* are cosmopolitan. *Launaea* ranges from South Africa to central Asia and temperate Europe. There are six other genera occurring from Europe to central Asia, six from Europe to temperate Asia and North America and four in western and central Asia. This distributional record seems to indicate that the Cichorieae are essentially an Old World group with an African-Eurasian-American distribution. There are nine genera, *Sonchus*, *Crepis*, *Lapsana*, *Hypochoeris*, *Mulgedium*, *Lactuca*, *Taraxacum*, *Prenanthes* and *Hieracium*, which occur on all these continents. It seems that along this African-Eurasian-American distribution-belt variation occurred particularly in the Mediterranean region, in China, and in the western United States.

2. The Tribes of Compositae in China

All the 13 tribes of Compositae are represented in the flora of China by either native or introduced species. Their size, as represented by the recognized genera, their effect in the appearance of the general flora and their prominence in the natural flora, as illustrated by the species/genus ratio, may be summarized in the following table.

TABLE I. The Tribes of Compositae in China [2]

Tribes	No. of genera	No. of species	Species/genus ratio	Large genera (10 or more species)	Small genera (9 or fewer species)	No. of endemic genera
Vernonieae	6	40	7−	1	5	0
Eupatorieae	4	24	6	1	3	0
Astereae	22	203	9+	3	19	9
Inuleae	19	229	12+	6	13	2
Heliantheae	24	46	2−	0	24	1
Helenieae	3	5	2−	0	3	0
Anthemideae	17	271	16−	3	14	4
Senecioneae	17	358	23−	5	12	7
Calenduleae	1	2	2	0	1	0
Arctotieae	1	1	1	0	1	0
Cynareae	23	439	19+	6	17	7
Mutisieae	6	71	12−	3	3	2
Cichorieae	24	340	15	10	14	3
Total	167	2029	12+ (average)	38	129	34

[2] No distinction is made here between native and introduced species. See text.

As indicated by the number of recognized genera the Heliantheae and the Cichorieae are the largest tribes of Compositae in China. However, their positions in the flora of China are very different. In the Heliantheae, with the exception of *Sheareria*, all the genera have been introduced through the intentional or accidental activities of man. Naturally, these introduced genera are small ones in the flora of China and their species/genus ratio for the tribe in China is less than two. Over two-thirds of these genera contain only one species each, and the others have two to six species. However, to a casual traveler who visits only the large cities or coastal areas of the country the members of this tribe may appear to be the most prominent feature in the general flora of the region. This is because the most commonly cultivated Compositae in the gardens of Chinese metropolises, (species of *Zinnia*, *Helianthus*, *Coreopsis*, *Dahlia* and *Cosmos*) are Heliantheae. Likewise, the most widespread weeds of the area, common in parks, gardens and school-yards (species of *Xanthium*, *Siegesbeckia*, *Eclipta*, *Bidens*, *Galinsoga* and *Wedelia*) also belong to this tribe. With the exception of these cultivated and weedy species, the other members of this tribe have a very limited distribution, being found chiefly in the warmer regions of the country. They occupy a very minor position as constituents of the natural vegetation in China.

Unlike the Heliantheae, the tribe Cichorieae is large both in the number and size of its included genera. The species/genus ratio for this tribe in China is fifteen. As illustrated in Table II, *Lactuca*, *Taraxacum*, *Crepis* and *Youngia* are the large genera in this tribe. Each of the first two genera

has fifty-seven species in China, and each of the other two genera has over thirty species. Moreover, the Cichorieae include the largest number of large genera among all the tribes of the Chinese Compositae. Many of these large genera, such as *Taraxacum*, *Lactuca*, *Youngia* and *Ixeris* contain relatively widespread species, some of which have become more or less weedy. The region on the borders of Yunnan, Szechuan, and Sikang (the Meridional Ranges) seems to constitute the area of the species concentration of many genera of this tribe. Maps 22 and 23 indicate that a large number of the species in the genera *Lactuca*, *Crepis* and *Youngia* occur in this region. According to Stebbins, this area is also the point of origin and the center of distribution of three endemic genera, *Dubyaea*, *Soroseris* and *Faberia*. He also maintains that *Dubyaea* is the most primitive genus of the tribe. Because of its large number of genera, its rather high species/genus ratio and its unique endemism, the Cichorieae contribute important elements to the composition of the natural vegetation of the country.

The next largest tribes of Compositae in China are the Astereae, Cynareae, Inuleae, Anthemideae and Senecioneae. Like Cichorieae these tribes are comparatively large for the number of their included genera. Senecioneae and Cynareae both have high species/genus ratios, while Astereae, Senecioneae and Cynareae contain the largest number of endemic genera. They are important elements in the natural vegetation of the country. The most striking feature lies with the Senecioneae. This tribe has the highest species/genus ratio among all the tribes of Compositae in China, and this high ratio is due to the large number of species of only four genera, namely, *Senecio* 160, *Ligularia* 105, *Cacalia* 60, and *Cremanthodium* 47. The center of concentration of species of these closely related genera is the Meridional Ranges. This region is not only the home of many endemic species of these large genera, it is also the site of many monotypic and oligotypic endemic genera of this and related tribes. Good's statement (1929, p. 313) concerning *Cremanthodium* in this region, "the present point of highest species concentration happens also to be the generic point of origin," could be applied to many genera of the Astereae, Cynareae, Inuleae, Anthemideae and Senecioneae, including the genus *Senecio*.

The tribe Mutiseae is a relatively small one in China. Nevertheless, the tribe is fairly well represented in the natural vegetation of the country. With the exception of *Gerbera* which has a South Africa-Madagascar-tropical Asia distribution with the Chinese species marking the northern limit of its range, all the other genera of Mutiseae in China are essentially Chinese. Three of them (*Leucomeris*, *Myripnois* and *Nouellia*) are genera endemic to China. The other two have ranges extending either from India to Japan (*Ainsliaea*) or from Afghanistan to Japan (*Pertya*) with China being the center of their distribution. Forty-seven out of a total of fifty species of *Ainsliaea* occur in China, and ten of the twelve species of *Pertya* are Chinese.

Vernonieae and Eupatorieae are poorly represented in China and those genera which do occur are essentially widespread tropical taxa. As weedy species they may produce quite a prominent effect on the general flora in

the warmer regions of China. With the exception of *Eupatorium* their distributions are very limited.

The Helenieae, Calenduleae and Arctotieae are represented in China only as cultigens.

II. THE GENERA OF COMPOSITAE IN CHINA

Two hundred and nineteen genera of Compositae have been recorded from China. Fifty-two of them belong to the doubtful and excluded category. The sizes and distributions of these genera within China and a comparison with the figures for the world are summarized in the following table. In this enumeration the genera are presented in the sequence of Dalla Torre and Harms. The numerals in the parentheses immediately following the names are those assigned by those authors. The names which do not have such numerals in parentheses are either invalid epithets or valid genera published after 1905. Most of the names in the latter group represent genera peculiar to the flora in China. The total number of species in each genus and the general area of distribution are chiefly adopted from Dalla Torre and Harms. A few of them are summarized from the *Index Kewensis*.

In presenting the distribution of the genera within China the following abbreviations are used. A = Anhwei, Cha = Chahar, Che = Chekiang, Chi = Chinghai, F = Fukien, H = Hainan, He = Heilungkiang, Hn = Honan, Hp = Hopei, Hun = Hunan, Hup = Hupei, J = Jehol, Kan = Kansu, Ki = Kiangsi, Kir = Kirin, Ks = Kwangsi, Kt = Kwangtung, Ku = Kiangsu, Kwe = Kweichow, L = Liaoning, M = Mongolia, N = Ninghsia, Sa = Shansi, Se = Shensi, Si = Sikang, Sin = Sinkiang, St = Shantung, Sy = Suiyuan, Sze = Szechuan, T = Taiwan, Tib = Tibet and Y = Yunnan.

In the remarks column the word "endemic" refers to the genus or species described from or limited to China.

Genera known only in cultivation or as adventives are in large and small capitals. Synonyms and other excluded names are in italics.

TABLE II. **An Enumeration of the Genera of Compositae in China**

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Vernonieae					
ETHULIA (6)	3	Trop. As, Afr, Mad.	1	1	T; adventive.
Vernonia (23)	450	Am, Afr, Mad, trop. As.	55	34	See map 1, 20 spp. endemic.
Camchaya	3	Indo-China, Siam	1	1	Y.
STOKESIA (35)	1	N. Am.	1	1	Cultivated.
ELEPHANTOPUS (47)	16	Pantrop; Am, espec.	5	2	T, Kt, H, Sze; adventive.
PSEUDOELEPHANTOPUS	1	Pantrop.	1	1	T; adventive.

* * * * *

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Eupatorieae					
Adenostemma (57)	6	Pantrop.	4	2	T, Kt, H, Che, Hup, Kwe, Y, Sze, Hp.
AGERATUM (67)	30	Trop. N. Am.	3	2	T, F, Kt, H, Che, Y, Sze; cultivated, naturalized.
Eupatorium (88)	400	Am, Eur, As, Afr.	28	17	See map 2.
Mikania (90)	150	Pantrop; Am, espec.	4	3	Kt, H, T.
		* * * * *			
Astereae					
Solidago (121)	80	N. Am.	6	5	Kt, Hun, Kwe, Y, T, Kir, Ku, Mong, Sin.
Pteronia (134)	50	S. Afr.	1	0	Chinese sp. transferred to *Vernonia*
Dichrocephala (138)	5	Afr, trop. As.	8	3	T, F, Kt, H, Y, Kwe, Sze, Tib.
Cyathocline (139)	2	India to s. China.	1	1	Kt, Kwe, Y.
Grangea (137)	3	Trop. As, Afr.	3	2	T, Kt, H.
Lagenophora (146)	12	Trop. As, to Austr.	3	1	T, Kt.
Rhynchospermum (147)	1	India, Malaya.	2	1	T, Y; monotypic.
Myriactis (148)	10	E. Himal. reg.	9	5	Y, Sze, T, Kwe; natural distribution.
BELLIS (151)	10	Medit. reg.	1	1	Cultivated.
CALOTIS (157)	16	Austr.	1	1	H; adventive.
Asteromoea (165)	11	E. Asia.	11	10	Kt, Hun, Y, Sze, Sa, Se, St, Hp, Ku, F, Che, Ki, Hup.
Kalimeris	7	E. Asia.	7	0	Transferred to *Asteromoea.*
Martinia	1	E. Asia.	1	0	Transferred to *Asteromoea.*
Callistephus (170)	2	E. Asia.	2	1	Cha, Tib, Hp, Sa, Kir, He; endemic.
Callistemma	2	E. Asia.	2	0	= *Callistephus.*
Boltonia (164)	5	N. Am.	6	0	Misidentified; Chinese material = *Asteromoea.*
Heteropappus (168)	6	E. Asia.	10	5	St, He, M, Che, T, Kir, Kw.
Arctogeron	1	Mongolia.	1	1	M; endemic.
Wardaster	1	W. China.	1	1	Si; endemic.
Aster (172)	200	Am, As, Eur, S. Afr.	204	137	See map 3.
Calimeris			9	0	= *Aster.*
Diplopappus			4	0	= *Aster.*
Rhinactina			2	0	= *Aster.*
Turczaninovia			1	0	= *Aster.*
Asterothamnus	7	NW. China.	7	7	
Pseudolinosyris	2	Centr. Asia.	2	0	Not in Chinese territory now.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Galatella	25	Centr. Asia.	17	7	Si, M.
Brachyactis	13	Centr. Asia.	3	3	Hp, Se, Kan, Sin, J, Sy, Si, Tib.
Heteroplexis	1	S. China.	1	1	Ks; endemic.
Erigeron (173)	150	Am, As, Eur, Austr.	40	25	See map 4.
Microglossa (193)	10	Trop. As, Afr, Mad.	3	3	Kwe, Y, Sze
Vierhapperia	1	Monotypic.	1	1	Y; endemic.
Conyza (198)	50	Pantrop.	36	7	T, F, Y, Sze, Che, Kwe; indicates extent of tropical elements.
Thespis (199)	1	Himal. reg.	1	1	Y.
		* * * * *			
Inuleae					
Cava	1	W. China.	1	1	Tib, Sze; monotypic.
Blumea (211)	60	Trop. Afr, As, Austr.	59	30	See map 5; 10 endemics.
Bileveillea			3	0	= *Blumea*.
Leveillea			3	0	= *Blumea*.
Blumeopsis	2	Indo-China.	1	1	H, Y.
Laggera (212)	10	Afr, As, Austr.	6	2	T, Y, Sze, Hup.
Pluchea (213)	30	Pantrop.	7	3	T, Kt, H, Sze.
Epaltes (225)	10	Pantrop.	2	2	Kt, H.
Poilania	1	Indo-China.	1	0	= *Epaltes*.
Sphaeranthus (227)	17	Afr, As, Austr.	8	3	T, Kt, H, Y.
Pterocaulon (229)	12	Am, Austr, Maurit, Mad, India	1	1	H.
Evax (238)	15	Med. reg, As, N. Am.	1	1	Sin.
Filago (241)	12	Eur, N. Afr, As, Am.	3	3	Tib, Sin.
Leontopodium (254)	ca. 70	Eur, As, Am, S. Am, Japan.	63	57	See map 6.
Anaphalis (255)	70	Eur, As, N. Am.	67	51	See map 7.
Antennaria (250)	15	Eur, As, Austr, Am.	5	2	Sin, M, Sze.
Phagnalon (260)	20	Canary Is, Med. reg, Abyss, Himal. reg.	1	0	Not in Chinese territory now.
Gnaphalium (264)	120	Pantrop.	52	20	See map 8.
HELICHRYSUM (278)	300	Eur, Afr, Austr.	2	2	1 cult, 1 Sin; introduced
Tugarinovi	1	N. China.	1	1	Sy; endemic.
Inula (333)	90	Eur, As, Afr.	42	28	See map 9.
Duhaldea	1	S. China.	1	0	= *Inula*.
Vicoa	16	Centr. As. to trop. Afr.	1	1	Y.
Pulicaria (350)	30	Med. reg, Eur, As, S. Afr.	4	4	Sin, Tib, Kwe.
Carpesium (353)	30	Eur, As.	30	18	T, Kt, H, Che, Ku, Hun, Hup, Y, Sze, Kwe, Sa, Kan, Si, Hp, Se, St, Tib, Kir.
Adenocaulon (354)	4	Himal. Reg, Am, Chile.	4	2	St, Kir, Sa, Cha.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Buphthalmum (364)	7	Eur, W. As.	1	0	Chinese material transferred to *Chrysanthemum*.
Anisopappus (368)	3	Trop. Afr.	2	1	Kt, H.
		* * * * *			
Heliantheae					
Sheareria (389)	2	Centr. China.	2	2	Che, Kt, Ki, Hup, Hun; endemic.
AMBROSIA (417)	15	Am, Med. reg, Afr.	1	1	Introduced.
Xanthium (419)	15?	Cosmopolitan.	7	2	Widespread.
ACANTHOSPERMUM (401)	3	Trop. Am.	1	1	Y; introduced.
PARTHENIUM (409)	9	N. & Centr. Am.	1	1	Kt; introduced.
ZINNIA (424)	12	N. & Centr. Am.	3	3	Cultivated.
SANVITALIA (427)	8	N. Am.	1	1	Kt; introduced.
HELIOPSIS (428)	7	N. & Centr. Am.	1	1	Cultivated.
Siegesbeckia (431)	10	Pantrop.	8	4	2 widespread, 2 ± localized.
ENHYDRA (435)	9	Centr. & S. Am, Austr.	1	1	H; introduced.
Eclipta (437)	4	S. Am, Austr; 1 sp. cosmopolitan.	1	1	Widespread; troublesome weed.
RUDBECKIA (449)	30	N. Am, Mex.	1	1	Cultivated.
Blainvillea (461)	9	Pantrop.	1	1	H.
Wedelia (463)	60	Pantrop.	6	5	T, Kt, Y, H, Sze.
Wollastonia			3	0	= *Wedelia*
TITHONIA (467)	10	Centr. Am.	1	1	Cultivated.
HELIANTHUS (471)	60	N. & Centr. Am.	6	4	Cultivated.
Spilanthes (478)	30	Am; 2 pantrop.	3	2	T, H, Y; 1 endemic.
SYNEDRELLA (495)	2	Trop. Am.	1	1	T, H, Kt
COREOPSIS (498)	70	Am, trop. Afr, Hawaiian Is.	7	3	Cultivated.
DAHLIA (499)	9	Mexico.	1	1	Cultivated.
GLOSSOGYNE (505)	5	Trop. As, Austr.	2	1	T, F, Kt, H; introduced.
Bidens (508)	90	Cosmopolitan, espec. Am.	17	6	Widespread; many vars.
COSMOS (509)	20	Am.	1	1	Cultivated.
GALINSOGA (517)	4	Am.	1	1	Szc, Y, Kt; newly introduced weed.
TRIDAX (516)	20	Centr. Am.	1	1	T; newly introduced.
		* * * * *			
Helenieae					
HELENIUM (576)	30	Am.	1	1	Cultivated.
GAILLARDIA (577)	12	Am.	2	2	Cultivated.
TAGETES (582)	20	Am.	2	2	Cultivated.
		* * * * *			
Anthemideae					
ANTHEMIS (601)	100	Eur, Med. reg, Abyss, As, Am.	6	4	North China.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Handelia	1	Monotypic.	1	0	Not in Chinese territory.
Achillea (603)	100	N. hemisphere.	14	10	See map 10.
Ptarmica			6	0	= *Achillea.*
Matricaria (610)	50	Med. reg, S. Afr, Eur, As.	14	4	He, St, Hp, L.
Allardia (614)	2	Centr. As.	2	2	Tib, Sin; endemic.
Waldheimia	2		2	0	= *Allardia.*
Formania	1	China.	1	1	Y; endemic.
Filifolium	1	N. China.	1	1	Hp, to He; endemic.
Brachanthemum	5	Centr. As.	5	5	Sin, M, Kan; arid regions.
Chrysanthemum (612)	200	Eur, As, Afr, Canary Is.	96	73	See map 11.
Pyrethrum (612b)	50?	Centr. & W. As.	18	5	Sin.
Tanacetum	130	Centr. & W. As.	44	0	= *Chrysanthemum*
Cancrinia (633)	9	Centr. As.	4	3	Sin, Tib, Y, Kan.
Cotula (622)	50	Temp. & subtrop. reg.	4	2	T, Kt, Hup, Sze.
Soliva (623)	6	S. Am, Austr, N. Am.	1	1	T; adventive.
Centipeda (624)	5	Austr. trop. As. Mad, Chile.	1	1	T, Kt, H, Che, Ku, Hun, Sze, Hp, St; widespread weed.
Myriogyne	1		1	0	= *Centipeda.*
Sphaeromorphaea	1	India, Siam.	1	1	T; adventive.
Crossostephium (630)	1	Luzon, E. As.	1	1	T, Kt; monotypic.
Stilpnolepis	1	Monotypic.	1	1	Sy; endemic.
Artemisia (629)	200	Cosmopolitan.	186	156	See map 12.
		* * * * *			
Senecioneae					
Stereosanthus (650)	4	China.	5	4	Y, Sze, Si; endemic.
Nannoglottis (649)	2	China.	2	2	Kan, Y; endemic.
Tussilago (651)	1	N. Afr, Eur, As, Am.	5	1	Y, Sze, Hp, Sy, Se, Kan, Sin.
Petasites (652)	14	N. hemisphere.	10	9	T, Ku, Hup, Sze, St, M, Y, Se, Si.
Nardosmia	19	N. hemisphere.	3	0	= *Petasites.*
Erechtites (660)	15	Trop. Am, Austr, N. Zeal.	2	2	T, H, Y, Ks, Kt.
Doronicum (671)	25	N. hemisphere.	6	3	Y, Sze, Si, Se, Kan, N, M, Sin, Tibet.
Gynura (676)	25	Trop. As, Austr, Afr.	26	16	T, H, Sze, Si, Kt, Y, Kwe, Hup, Che, Se, A.
Emilia (682a)	40	Trop. Afr, Mad, trop. As.	10	3	Kt, Che, westward to Y.
Cineraria (677)	25	S. Afr, Mad.	9	1	Largely transferred to *Senecio* or *Ligularia.*

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Cacalia (680)	70	As, N. & Centr. Am.	67	60	Widespread; not in F, Kt, H; endemic sp.
Parasenecio	1		1	0	= *Cacalia*.
Syneilesis	4	China.	4	4	Kir, He, Che, A, T; see *Senecio*.
Chlamydites	1	Monotypic.	1	1	Tib; endemic.
Senecio (682)	1200	Cosmopolitan.	363	160	See map 14.
ARNICA (667)	20	N. Am, Eur.	3	1	Cultivated.
Ligularia (683)	150	Eur, As.	125	105	T, Y, Sze, Si, Kan, Kwe, Sa, M, Sin, Tib, L, Kir, Ki, St, Hn, Che, Hun, Hup, Hp, Chi, He, Sy, Cha, J.
Farfugium	3	E. As.	4	1	T, Kt, Che, Hup.
Senecillis	70	Centr. & E. As.	45	0	= *Ligularia*.
Cremanthodium (684)	60	Himal. reg.	57	47	See map 15.
Werneria (686)	30	S. Am, trop. Afr.	2	0	Transferred to *Cremanthodium*.
		* * * * *			
Calenduleae					
CALENDULA (694)	15	Med. reg. to Persia.	2	2	Cultivated.
		* * * * *			
Arctotieae					
ARCTOTIS (703)	60	S. Afr.	2	1	Cultivated, recent introduction.
Gorteria (704)	4	S. Afr.	1	0	Misidentified.
		* * * * *			
Cynareae					
Echinops (713)	60	E. As, S. Eur, Med. reg., S. Afr.	15	11	Lower Yellow River.
Xeranthemum (716)	6	Med. reg., W. As.	2	0	= *Helichrysum* or *Blumea*.
Atractylis (721)	15	Canary Is, Med. reg., N. Afr.	9	8	North of Yangtze, lower Yellow River.
Atractylodes			8	0	= *Atractylis*.
Giraldia			1	0	= *Atractylis*.
Arctium (723)	6	Eur, As, N. Am.	3	2	N. China to Sin.
Cousinia (724)	250	Centr. As.	2	2	Tib, Sin; arid regions.
Xanthopappus (726)	2	NW. China.	2	2	Chi, Si, Kan; endemic.
Takeikadzuchia	1	N. China.	1	1	Cha; endemic.
Olgaea	11	N. China.	11	9	M, Kan, N, Sa, Sin, Hp; endemic.
Alfredia	11	Centr. As.	3	0	Not in Chinese territory.
Carduus (732)	100	Eur, Afr, As.	19	11	See map 16.
ONOPORDON (738)	20	Afr, Eur, W. As.	1	1	Sink.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Cnicus (750)	1	Eur, As.	32	0	Transferred to *Cirsium*.
Cirsium (733)	150	N. Afr, Eur, As, N. & Centr. Am.	70	59	Widespread.
Cephalonoplos	4	E. As.	3	3	St, Sa, Se, Kir, He, L, J, Cha, Sy, Tib; a segregate from *Cirsium*.
Cynara (734)	12	Med. reg.	2	2	Cultivated; recent introduction.
Hemistepta	1	E. As.	1	1	T, Kt, Ku, Y, Sze, St, Hn, Hp, Se; monotypic, a common weed.
Saussurea (728)	125	N. hemisphere, Austr.	338	270	See map 17; largest genus in China.
Bolocephalus	1	Monotypic.	1	1	Si; endemic.
Vladimiria	1	Monotypic.	1	1	Y; endemic.
Mazzettia	1		1	0	= *Vladimiria*.
Jurinea (730)	50	Centr. & S. Eur, N. Afr, W. & Centr. As.	18	18	Y, Sze, Tib, Sin.
Tricholepis (744)	12	Himal. reg.	1	1	Y, Tib.
Synurus	8	Temp. As.	4	3	Che, Ki, Hup, St, Hp, Se, Kir, He.
Silybum (735)	2	Canary Is, Med. reg. to Persia	1	1	Introduced.
Serratula (745)	40	Eur. to Japan	43	19	See map 18.
Leuzea			1	0	Transferred to *Rhaponticum*.
Rhaponticum			1	1	Hp, Se, Kir, He, Cha.
Centaurea (747)	500	Med. reg., Eur, As, N. & S. Am, Austr.	8	7	Sin, Ku, Hn, to M, Tib, Kan.
Carthamus (748)	20	Med. reg. to Centr. As.	1	1	Cultivated in W. China.
		* * * * *			
Mutisieae					
Leucomeris (756)	2	E. Himal. Reg.	1	1	Y.
Pertya (775)	12	Afghan. to Japan	12	10	Y, S, Kan, to Che, Kt.
Myripnois (782)	2	China.	3	2	Hopei to Kansu, endemic.
Ainsliaea (783)	50	India to Japan.	58	47	Y, Sze, due east to Taiwan.
Nouelia (791)	1	Monotypic.	1	1	Y, Sze; endemic.
Gerbera (798)	40	S. Afr, Mad, trop. As, Tasmania.	18	10	Kt, Hun, Hup, Y, Kwe, Sze, St, Hp, Sa, Se, Kan, M, St, N, Kir, Cha; 2 widespread, the others endemic.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Leibnitzia	5	E. As.	4	4	T, Kir, He, J, Y, Tib; segregate from *Gerbera*.
Anandria	6	E. As.	2	0	Misidentified; = *Gerbera*.
		* * * * *			
Cichorieae					
CICHORIUM (823)	8	Med. reg. to temp. As.	2	2	Ku, St, Hp, Sa, Se, Sin; cultivated or weeds.
Lapsana (825)	9	Eur, As, Am.	3	3	Kt, Che, Ku, Ki, Hup, Sze, Se; 1 widespread along Yangtze, 2 localized, coastal.
Koelpinia (832)	3	Med. reg., Afr, Centr. As.	1	1	Sink.
Acanthocephalus	2	Centr. As.	1	0	Not in Chinese territory now.
Rhagadiolus	8	Centr. As.	1	0	Not in Chinese territory now.
Hypochoeris (842)	50	Eur, Med. reg, N. As, N. Am.	4	3	Kir, He, Jehol, St, Hp, L.
Heteracea	1	Centr. As.	1	0	Not in China.
Tragopogon (849)	40	Eur, Med. reg, W. & centr. As.	10	10	See map 20; Centr. Asian element.
Scorzonera (851)	100	Eur, Med. reg, W. & Centr. As.	20	18	See map 20.
Picris (845)	40	Eur, Med. Reg, Abyss, temp. As.	9	8	Kir, He, Y, Sze, St, Sin, Kt, Kan; 1 widespread, 2 endemic.
Lagoseris	32	centr. & W. As.	1	0	Not in China.
Taraxacum (862)	1200?	Cosmopolitan	67	57	See map 21.
Leontodon	123	Eur, centr. & W. As.	8	0	Chinese spp. = *Taraxacum*
Chondrilla (860)	18	Eur, As.	3	3	Sin, Kan.
Sonchus (865)	45	Cosmopolitan	19	10	Widespread; weedy.
Launaea (863)	30	Med. Reg, S. Afr, trop. As, E. Indies	5	4	H, Y, Sze.
Lactuca (866)	150	Cosmopolitan.	112	81	See map 22.
Mycelis	5	E. As.	2	0	= *Lactuca*.
Cicerbita	60	Centr. As.	7	7	Y, Si, Sze.
Mulgedium	7	Centr. As.	2	0	= *Lactuca*.
Soroseris	9	W. China.	9	9	Y, Sze, Kan, Chi, Sin; endemic.
Prenanthes (876)	30	Eur, Med. reg, Canary Isl, As. Am.	25	19	Y, Sze, Si, Tib, Hup, Hun, Kan, Se, Sa, St, Hp, Cha, Kir.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Faberia (872)	6	W. China.	7	6	Y, Sze, Kwe; endemic.
Crepis (875)	200	N. hemisphere.	83	31	See map 23.
Barkhausia			4	0	= *Crepis*.
Geblera			2	0	= *Youngia*.
Youngia	35	Himal. reg. to Japan.	39	30	See map 22.
Ixeris	20	Himal. reg. to Japan.	26	14	See map 23; common weed.
Crepidiastrum	7	E. As.	4	3	T, Che.
Dubyaea	12	E. Himal. reg.	12	7	Y, Sze.
Hololeion	3	Japan.	1	1	Ku.
Hieracium (877)	400	Eur, Am, Afr, As.	17	14	Ku, Ki, T, Sze, Kwe, Sin, Hp, M, Se, St, Kir, He, Cha, Sy; mostly isolated spp. known from one collection.
Crepidiastrixeris	3	Japan, E. China.	1	1	Che; a hybrid genus.

With the exclusion of the doubtful and invalid genera there are only 167 genera of Compositae in China. Most of these genera are small. Fifty-seven of them have only one species each, and 40 others have 2 or 3 species each. The largest of all is *Saussurea* with 279 species. The next in size are *Senecio* with 160 species, *Artemisia* with 156, *Aster* with 137 and *Ligularia* with 105 species. Some botanists, such as Franchet, interpret *Senecio* in a broader sense and place *Ligularia*, *Cacalia* and *Cremanthodium* in it as sections. In this broader sense, *Senecio* would have 372 species in China and thus become the largest genus of Compositae in that country, as it is also the largest genus of the Compositae in the world.

1. The Large Genera and Their Distributions

Only 38 genera of the Chinese Compositae contain ten or more species. For convenience of discussion, these are called the "large genera." They are scattered in the Vernonieae, Eupatorieae, Astereae, Inuleae, Anthemideae, Senecioneae, Cynareae, Mutisieae and Cichorieae (Table I). By plotting the occurrence of all the species of a large genus on an outline map of China, striking distributional patterns of these large genera are revealed. In these maps circles represent species occurring only in one province and the dots denote species recorded from two or more provinces. The combined number of circles and dots within the confines of a province gives the total number of species of the genus under discussion in that province. Thus a distribution map for a given genus tells both its range and its area of concentration of species. In a few cases two relatively

small genera are plotted on one map. Triangles are used to represent the species of the second genus, with the white ones indicating local endemics and the solid ones species of wider range.

Vernonia is a genus of wide range with species in the Americas, Africa, Madagascar, and tropical Asia. In China there are thirty-four species, with a concentration in Taiwan, Kwangtung, Yunnan and Szechuan. Ten of these thirty-four have an Indo-Malaysian range, two of them extend to Java, and twenty of them are endemic to China. Six of these endemics occur in Yunnan (MAP 1). In general *Vernonia* is a southern genus and its range does not reach north of the Yangtze River.

Eupatorium is another widespread genus with many species, especially in Central and South America, Africa, Europe and Asia. In China there are seventeen species, and most of them are evenly distributed from Hainan to Heilungkiang (MAP 2). Endemism is relatively low. Taiwan seems to have the largest species concentration. It is interesting to note that this genus is absent in the northern and western half of the country.

Aster is the third largest genus of Compositae in China. It contains 137 species occurring in every province of the country. The centers of species concentration are Yunnan (51 species), Szechuan (48 species), Sikang (30 species), Kansu (20 species) and Hopei (20 species). Taiwan has 15 species. Considering the small size of the island, the genus is very well represented there. This genus has many widespread species in China. For example, *A. ageratoides* and its varieties occur in twenty-three provinces and *A. altaiacus* and its varieties occur in nineteen provinces. Many species share the Yunnan-Szechuan-Kansu range. Local endemism is high for the genus. Of the endemic species, Yunnan, with its 15 species, has the highest number, Szechuan has 13, Taiwan 10, Tibet 9, Kansu 6, Sikang 5. It is interesting to note that the species in Sinkiang are all widespread, while nearly half of the 21 species in its neighboring province, Tibet, are local endemics (MAP 3).

Erigeron is a widespread genus with species occurring in America, Australia, Asia and Europe. In China there are twenty-five which are fairly evenly distributed throughout the country. They are absent from Ninghsia, Kansu, Chinghai and Tibet (MAP 4). There are several weedy species which occur in extensive areas. For example, *E. acer* occurs in ten provinces from Hupei and Szechuan due north to Kirin and westward to Sinkiang. *E. canadensis* has an even wider range, occurring in fourteen provinces from Taiwan-Kwangtung northward to Kirin and thence due west to Sinkiang. This genus has very few endemic species. Half of the eight endemics are in the Altai region.

Blumea is a genus with an African-Asiatic-Australian range. In China there are thirty species which concentrate in Taiwan, Kwangtung, Hainan,

MAPS 1–8. The geographical ranges in China of eight large genera of Compositae in the tribes Vernonieae, Eupatorieae, Astereae, and Inuleae.

Yunnan and Kweichow (MAP 5). Most of the species have an Indo-Malaysian distribution. In China they occur largely in the few border provinces where there are port cities. The large number of endemics in Kweichow (50%) is evidently due to the careless work of Léveillé and Vaniot who published too many species from fragmentary collections. *Blumea* serves as a good example of the route of migration and the area of extension of tropical elements in the flora of China.

Leontopodium is a discontinuous genus occurring in the high mountains or high latitudes of Europe, Asia and South America. In China there are 57 species which are concentrated in Yunnan, Szechuan, Sikang and Tibet, and thence northeastward through Kansu, Shansi, Chahar to Heilungkiang and Mongolia. In the mountains of the Meridional Ranges there are many endemics and hybrids (MAP 6). It is very likely that this region is both the center of concentration and the place of origin of the genus. For example, *L. kamtschaticum,* as is indicated by many recent collections, is concentrated in Sikang; thence it extends westward to Tibet, and northeastward to Szechuan, Kansu, Chahar, Mongolia, Heilungkiang, Far Eastern Russia and Kamchatka. It is evident that although the species was first described from Kamchatka, this peninsula is only on the periphery of its range. *Leontopodium japonicum* tells almost the same story. It is very likely that the species originated in the west, somewhere in the mountains on the Kansu-Shensi-Szechuan border, thence it extended eastward through Hupei and Anhwei to Japan or through Hopei and Korea to Japan. These are common routes for the migration of many Sino-Japanese species.

Anaphalis is another genus which has a discontinuous range and which has its concentration of species in the Meridional Ranges of China. It has been recorded from Europe, Asia and North America, but the bulk of the species are in China. There are 51 species, many of them local endemics, concentrated in Yunnan, Szechuan, Sikang and Kansu (MAP 7).

Gnaphalium is a genus of the warm regions throughout the world. In China there are twenty species, rather evenly distributed from Hainan to Heilungkiang. Although there are a few endemics in Yunnan, Sikang and Tibet, there is no region which can be considered as the center of concentration of species for this genus. There are a few widely spread species. For example, *G. affine* extends from Taiwan to Nepal, occurring in fifteen provinces in China. It is a very tough species and colonizes all sorts of waste places, even the perpendicular cracks of dry hard city walls. *G. hypoleucum* is another widespread species which extends from Taiwan to Nepal. It occurs in eight provinces. It is interesting to note that in China the species occurs only in areas where there are large centers of commercial or political activity (MAP 8).

Inula is an Old World genus with species occurring in Africa, Europe and Asia. In China there are twenty-eight species which are evenly dis-

tributed in the temperate and the mid-high altitudes of the subtropical regions (Map 9). It seems that Yunnan, Szechuan and Kweichow constitute the center of the species concentration. In Yunnan and Kweichow almost half of the species are endemics. There are a few widespread species. For example, *I. britannica* and its varieties occur in fifteen provinces north of the Yangtze River and *I. cappa* occurs in six provinces south of the same river. Several species of this genus are very good indicators of the types of vegetation in China. In addition to *I. britannica* and *I. cappa,* which have a northern or a southern distribution, *I. salsoloides* expresses a special floristic relationship between Hopei, Chahar, Suiyuan, Ninghsia, Shansi, Shensi, Kansu, Chinghai and Sinkiang, and *I. serrata* illustrates the floristic affinity between Sikang, Yunnan and Kweichow.

Carpesium is a genus of the north temperate or subtropical regions of the Old World. Its range extends from Europe through Asia to Japan. It has eighteen species in China. It seems to have two centers of concentration, the one being Yunnan, Szechuan, Sikang, Hupei, Shensi, Shansi and Hopei and the other being Taiwan and Kwangtung. There are several widespread species. *Carpesium abrotanoides* occurs in twelve provinces, from Taiwan-Kwangtung westward to Yunnan and Sikang and thence due north to Shensi and Hopei. *Carpesium cernuum* shares the same range, but extends even more northward to Kirin. There are relatively fewer local endemic species in this genus.

Achillea is a widely distributed genus of the northern hemisphere. There are 10 species in China. With the exception of a southern variety of *A. sibirica,* which occurs in Kweichow and Yunnan, and an Eurasian-American species, which was recorded from Chekiang, the genus is restricted to the north of the Yangtze River (Map 10). Its distribution is a good illustration of the southern limit of the northern elements in the flora of China.

Chrysanthemum is a large genus with species occurring in Europe, Canary Islands, Africa, temperate Asia and America. In China there are seventy-three species, many of which are local endemics known only from the type collection. Most of the endemic species are in Sikang, Yunnan, Szechuan, Kansu, Shensi, Shansi, Mongolia and Sinkiang (Map 11). The taxonomy of this group is in bad shape, and it is highly possible that many of the endemics described as species in this genus are merely local variants of a few species. It is interesting to note that the genus is poorly represented in low altitudes of South China. *Chrysanthemum indicum* is a widespread species recorded from thirteen provinces.

Artemisia is a cosmopolitan group which in China is the second largest genus of Compositae. Its 156 species represent every province of the country. As far as the number of species in each province is concerned, Hopei takes the lead with 59 species, 3 of which are local endemics. Yun-

MAPS 9–16. The geographical ranges in China of eight large genera of Compositae in the tribes Inuleae, Anthemideae, Senecioneae, and Cynareae.

nan has 50 species, 11 of which occur in that province alone. Szechuan has 41 species, 5 of which are local endemics. Taiwan has 25 species, 7 of which are endemics. Considering the small size of the island, the genus is very well represented there. In fact, *Artemisia* is the only genus of Compositae that has been recorded from every province (Map 12). This genus needs revision; many local variants, apomictic or polyploid forms have been named as species and, consequently, many taxa show anomalous patterns of distribution. For example, *A. dubia* var. *septentrionalis* has been recorded from Hainan, Kweichow and Hopei, and *A. handel-mazzettii* has been recorded from Yunnan and Hopei only. Such disjunction is not known in any other species of flowering plants in China.

Gynura has an African-Asiatic-Australian distribution. There are 16 species in China. With the exception of *G. ovalis* var. *pinnatifida*, which extends into the southern part of Shensi, all the rest are distributed to the south of the 30°N. parallel. Thus the species of *Gynura* serve as good examples for showing the northern limit of the range of southern elements in the flora of China.

Cacalia is an Asiatic-American genus. Its species occur in Asia, North America, Central America and the West Indies. In China there are 60 species which are distributed in high altitudes and mid-latitudes. Yunnan, Szechuan, Sikang, Kansu, Shensi, Shansi, Hupei, Hopei and Honan seem to be the center for the concentration of the species. It has a high percentage of endemism (Map 13). Forty per cent of the species in Yunnan are known only from the type material. All the species in Taiwan are endemics. *Cacalia* is morphologically closely related to *Senecio* and *Ligularia*. The distributional patterns of these three genera are also similar. It is worthy of note that this is the only genus that has 5 species in Honan, a province in which other genera of Compositae are relatively poorly represented.

Senecio is the largest genus of Compositae, and a very heterogenous one. Its species occur in all parts of the world. In China, because of the recognition of *Cacalia*, *Ligularia* and *Cremanthodium*, all of which are included in this genus by some authors, *Senecio* becomes the second largest genus. However, if Franchet or James Small's interpretation of the genus were adopted, *Senecio* would be the largest genus in China. The concentration of species of this genus is in Yunnan, Szechuan, Sikang, Kweichow and Hupei (Map 14). In Yunnan alone there are 73 species, 41 of which are known only from that province. Szechuan has 51 species, 12 of which are local endemics. Sikang has 13 species, 6 of which are local endemics. Kweichow has 23 species, 7 of which are not known elsewhere.

Ligularia is a genus with European-Asiatic distribution. In China there are 105 species highly concentrated in Yunnan, Szechuan, Kansu and Hopei. In Yunnan alone there are 50 species, 27 of which are known

only in that province. Szechuan has 49 species, 14 of which are local endemics.

Cremanthodium is an endemic genus of the Meridional Ranges. Its distribution extends to the Himalayan Region. In China there are 47 species concentrated in Yunnan, Sikang, Szechuan, Tibet and Kansu (MAP 15). There are 38 species in Yunnan, about one-fourth of which are endemic to that province. Within China this genus is strictly limited to the Southwest. Its closely related genera *Cacalia*, *Senecio* and *Ligularia* are all well represented in Taiwan, but the range of *Cremanthodium* extends hardly beyond the Long. 110° E.

Echinops is an Old World genus with species occurring in southern Europe, the Mediterranean region, tropical Africa and eastern Asia. There are 11 species in China distributed north of the 35° N. parallel (MAP 16). Judging from the specimens in the Gray Herbarium, the center of concentration of the species appears to be western and central Asia. China is only on the periphery of its range. Several species have a considerably wider range. For example, *E. latifolius* extends from Dahuria to Honan, and *E. gmelinii* covers almost the same area. There are four endemic species known only from their type collections.

Carduus is another European-African-Asiatic genus. There are eleven species in China, two of them with wide ranges. *Carduus acanthoides* occurs in six provinces from Yunnan-Kweichow northward to Kansu and Hopei. *Carduus crispus* has an even wider range, occurring in 16 provinces from Chekiang westward to Szechuan and northward to Heilungkiang and Mongolia. The other species are local endemics (MAP 16).

Cirsium is a widespread genus with species occurring in North Africa, Asia and North and Central America. There are 59 species in China. They are distributed throughout the country. Yunnan, Szechuan, Kweichow and Taiwan are areas of high endemism. Yunnan has 22 species, 13 of which are confined to that province. Taiwan has 12 species, 7 of which are endemics. There are several widespread species. For example, *C. arvense* (first recorded from the Canary Islands), and its various varieties occur in 11 provinces, from Kiangsu to Heilungkiang and thence due west to Sinkiang. *Cirsium chinense* is another widespread species. Its range extends from Taiwan to Yunnan and northward to Shensi and Hopei. In most places it is a very troublesome weed.

Saussurea is a genus widely distributed throughout the northern hemisphere and the mountains of Australia. In China it constitutes the largest genus of the Compositae. There are 279 species, especially well represented in Yunnan, Szechuan, Sikang, Tibet, Hupei, Kansu, Shensi, Shansi, Hopei, Jehol, Kirin, Mongolia and Sinkiang (MAP 17). Yunnan alone has 94 species, 53 (almost 57%) of which are confined to that province.

There are 82 species in Szechuan. Twenty-six (almost 32 per cent) of them are local endemics. Twenty-two (a little over 43 per cent) of the 51 species from Sikang are endemic to that province. It is interesting to note that the genus is poorly represented in eastern and southern China, and it has never been recorded from Kwangsi, Hainan and Honan. It is evident that the species of this genus prefer high altitudes or high latitudes.

Jurinea is an Old World genus with species occurring in central and southern Europe, North Africa, western and central Asia. In China there are 18 species, all of which are local endemics (Map 18). They are known only from a few western provinces, and often only through the type collection.

Serratula is another Old World genus occurring in Europe and North Africa, thence due east to Japan. In China there are nineteen species distributed chiefly north of the Yangtze River. Some species also occur in Kirin, Heilungkiang, Mongolia and Sinkiang (Map 18).

Pertya is an Asiatic genus occurring from Afghanistan to Japan. There are ten species in China, all with very limited range (Map 19). Almost half of them are known only through the type material.

Ainsliaea is another Asiatic genus. Yunnan, Szechuan and Hupei constitute its center of distribution, and northern India and Japan are on the periphery of its range. There are 47 species in China (Map 19). Many of them are local endemics. For example, there are 22 species in Yunnan, 14 of which are endemic to that province. There are several species which indicate the relationship between the flora of Taiwan and the mainland of China. For example *A. fragrans* occurs in Taiwan, Kwangtung, Chekiang, Kiangsu, Kiangsi and Hopei. *Ainsliaea macroclinidioides* has the same range. In both cases the type localities are on the periphery of the range of the species. *Ainsliaea reflexa* and its varieties occur in Taiwan and also in Yunnan. This distributional pattern is common with many genera of woody plants.

Gerbera is a southern genus with species occurring in South Africa, Madagascar, tropical Asia and Tasmania. There are 10 species in China, and Yunnan and Szechuan again constitute the center of the species concentration. *Gerbera anandria* is a widespread species. It occurs in 15 provinces from Kwangtung northward to Kirin and Mongolia. A little over 45 per cent of the eleven species and varieties in Yunnan are endemic.

Tragopogon is an Old World genus with species occurring in Europe, the Mediterranean region, and western and central Asia. There are 10 species recorded from China. With the exception of three European species (one recorded from Nanking as a cultigen, and two from gardens in Peking) all the rest are localized in Sinkiang, especially the Tien-shan-Altai region

MAPS 17–23. The geographical ranges of seven large genera of Compositae in the tribes Cynareae, Mutisieae and Cichorieae. MAP 24. The distributions of small genera of Compositae in China. Dots = endemics, circles = adventives, and H = Himalayan genera.

(Map 20). *Tragopogon* is a good example of the extent of Central Asiatic elements in the flora of China.

Scorzonera is another Old World genus with species occurring in Europe, the Mediterranean region, western and central Asia, and thence due east to China, Korea and Japan. In China, there are eighteen species distributed in the arid regions of mid-high latitudes and the arid regions of Szechuan and Tibet (Map 20). The percentage of local endemics is low. Several species have wide ranges. For example, *S. albicaulis* occurs in twelve provinces from Chekiang westward through Hunan and Kweichow to Szechuan and thence due north through Honan, Shantung, Shensi and Hopei to Chahar, Liaoning and Kirin. *Scorzonera austriaca* occurs in eight provinces extending from Kiangsu northward through Honan, Shantung to Kansu and Mongolia. It is worthy of notice that in the distribution of *Senecio*, *Ligularia*, *Saussurea* and many other genera of Compositae, Yunnan and Szechuan are twin provinces in respect to high numbers of species, but this is not so with *Scorzonera*. Four species of *Scorzonera* have been recorded from Szechuan and none from Yunnan.

Taraxacum is a cosmopolitan genus of weedy species. The taxonomy of this genus is very difficult. When Handel-Mazzetti published his monograph of *Taraxacum* in 1907, he included 57 species. Index Kewensis lists in all over 1200 species, but binomials have been assigned to many apomictic forms. It is very hard to decide what is the approximate number of species of this genus in China. When Dahlstedt published H. Smith's collection in 1926 he added one-fourth more binomials to the Chinese *Taraxacum*. With the species added by Kitagawa in 1933–38, and Koroleva in 1940, 57 have been recognized from China. It seems that a large number of species are found in Yunnan, Szechuan, Tibet, Kansu, Sinkiang, Mongolia, Chahar, Liaoning and Kirin (Map 21). It is interesting to note that this genus is poorly represented in the warmer regions of China. It has not been recorded from Fukien, Kwangtung, Kwangsi or Hainan.

Sonchus is another cosmopolitan and weedy genus. There are 10 species in China, several of them widespread. *Sonchus arvensis* and its varieties occur in twenty provinces, from Taiwan and Kwangtung northward to Sinkiang, Mongolia and Kirin and *S. oleraceus* occurs in fourteen provinces, from Hainan northward to Kirin and westward to Sinkiang. Four local endemics have been recorded from Yunnan, Szechuan, Kweichow and Tibet. There seems to be no center of species concentration in China.

Lactuca is a cosmopolitan genus. There are 57 species in China distributed from Kwangtung and Hainan northward to Kirin and Heilungkiang. It seems that Yunnan, Szechuan and Kweichow form a center of concentration of species on the mainland, and Taiwan furnishes an area of diversification off the coast. A high percentage of endemism occurs

among species in both regions. In Yunnan there are 27 species, 17 (about 63 per cent) of which are endemics. In Taiwan there are 14 species, 11 (79 per cent) of which are endemics. There are a few widespread species: *L. indicus* and its varieties occur in 15 provinces, from Kwangtung northward to Kirin and *L. tatarica* occurs in 8 provinces, from Honan to Mongolia and westward to Sinkiang (MAP 22).

Prenanthes is a widespread genus with species occurring in South Africa, the Canary Islands, the Mediterranean Region, Europe, Asia, and America. The strongest development of this genus is in central and northern Europe. There are nineteen species in China. Yunnan, Szechuan and Kweichow again form the center of concentration of species. High ratios of endemism occur in Szechuan and Kweichow, where over 60 per cent of the species are known only from the type localities. There are a few widespread species. *Prenanthes brunoniana* and its varieties occur from northern India eastward through Yunnan, Kweichow to Hupei and Hainan. *Prenanthes tatarinowii* and its varieties occur in eight provinces from Hupei northward to Chahar and Kirin.

Crepis is a widespread genus with species occurring in the Canary and Madeira Islands, Europe, Africa, Asia, and North America. In China there are 31 species, concentrated in Yunnan, Szechuan, Kweichow, Sikang, Tibet, Sinkiang, and Mongolia (MAP 22). Yunnan seems to be the area of the highest species-diversification. It has not only the largest number of species but also the highest ratio of endemism (about 30 per cent). Most species have small ranges, usually limited to two or three provinces. For example, *C. rigescens* is limited to Yunnan and Szechuan, *C. tibetica* to Yunnan, Sikang and Tibet, *C. bodinieri* is confined to northern Yunnan and the adjacent area of Szechuan, and *C. chrysantha* to the Altai Region. As suggested by Babcock, *Crepis* is originally an Asiatic genus and the Altai region (northwestern Sinkiang and southwestern Mongolia) seems to be its center of origin. This region is still a part of the center of the concentration of species for the genus today. It is also worthy of note that *Crepis* is not represented in Taiwan, Fukien, Kwangtung, Hainan, Chekiang, Anhwei, Kiangsi, Shantung, Honan or Kirin.

Youngia is an Asiatic genus with species occurring from the Himalayan Region eastward to Japan. In China there are thirty species distributed from Hainan, Kwangtung and Taiwan, thence northward to Heilungkiang (MAP 22). Like *Crepis*, it has its center of species concentration in Yunnan and Szechuan, but it differs from *Crepis* in that it occurs also in the tropical regions. Again it differs from *Crepis* in that it has many widespread species. For example, *Y. japonica* and its varieties occur in thirteen provinces from Hainan, Kwangtung and Taiwan northward to Shantung, Hopei and Shensi. *Youngia sonchifolia* occurs in thirteen provinces from Chekiang to Szechuan and thence due north to Kirin and Heilungkiang.

Ixeris is another Asiatic genus with species distributed from the eastern Himalayan Region to Japan. In China there are fourteen species ranging from Hainan and Kwangtung northward to Heilungkiang (Map 23). Most of them are widespread weeds. For example, *I. chinensis* occurs in twenty-one provinces. Actually it is very difficult to determine the approximate number of species of *Ixeris* in China, since contemporary authors do not agree on the status of some of the taxa. The criteria for distinguishing *Ixeris*, *Youngia*, *Crepis* and *Lactuca* are not sufficiently strong and many species have been changed back and forth among these genera. For example, *I. chinensis* has been named *Prenanthes chinensis*, *Youngia chinensis* and *Lactuca chinensis*. Likewise, *Ixeris chinensis* ssp. *graminifolia* has been named *Ixeris graminifolia*, *Crepis graminifolia* and *Lactuca chinensis* f. *graminea* by outstanding synantherologists of our time.

Hieracium is a widespread genus with species in Europe, North and South America, North and South Africa, and northern and eastern Asia. There are fourteen species in China, distributed from Kiangsu, Kiangsi, Kweichow and Szechuan northward to Kirin, Heilungkiang and Sinkiang. Most of them have small ranges. *Hieracium umbellatum* is the only widespread species. It occurs in twelve provinces from Kiangsi-Hupei-Szechuan northward to Kirin, Heilungkiang, Mongolia and Sinkiang. According to Stebbins most of the Asiatic species are apomictic (Babcock, 1947, p. 83).

In conclusion, we may point out that the larger genera of Chinese Compositae evidently have four types of distribution. The first type, which is the most frequent, includes widespread genera with definite centers of species concentration. Twenty-two of the thirty-eight large genera (almost 57 per cent) have this type of distribution. *Aster*(T), *Leontopodium*, *Anaphalis*, *Artemisia*(T), *Inula*, *Chrysanthemum*(T), *Cacalia*(T), *Senecio* (T), *Ligularia*(T), *Cremanthodium*, *Cirsium*(T), *Saussurea*(T), *Jurinea*, *Gerbera*, *Ainsliaea*(T), *Prenanthes*, *Taraxacum*, *Lactuca*(T), *Crepis*, *Youngia*, *Pertya* and *Ixeris*(T) all belong here. The center of species concentration of all these genera is the Meridional Ranges. The genera marked (T) also have secondary centers of concentration in Taiwan. The second type comprises the northern genera with ranges limited to the north of the Yangtze River. Seven of the thirty-eight large genera (about 20 per cent) have this type of distribution. *Achillea*, *Echinops*, *Tragopogon*, *Scorzonera*, *Carduus*, and possibly *Hieracium* and *Serratula* belong here. Most of these genera also occur in Europe, the Mediterranean Region and central or western Asia. The third type includes the southern genera, the ranges of which are limited to the south of the Yangtze River. Of the thirty-eight large genera only *Vernonia*, *Eupatorium*, *Blumea*, and *Gynura* have this type of distribution. The fourth type includes those widespread genera which have no definite centers of species concentration. *Erigeron*, *Gnaphalium*, *Carpesium* and *Sonchus* exemplify this type of distribution and all include some widespread weedy species.

2. The Small Genera and Their Distributions

The small genera are taxa comprising one to nine species. This arbitrary classification is made merely for the convenience of discussion. There are 128 such small genera of Compositae in China. Their distribution among the tribes is given in Tables I and II. Most of these genera include one to three species, but a few have four or more species. The sizes of these small genera as indicated by the number of the included species are shown in the following graph (Fig. 2).

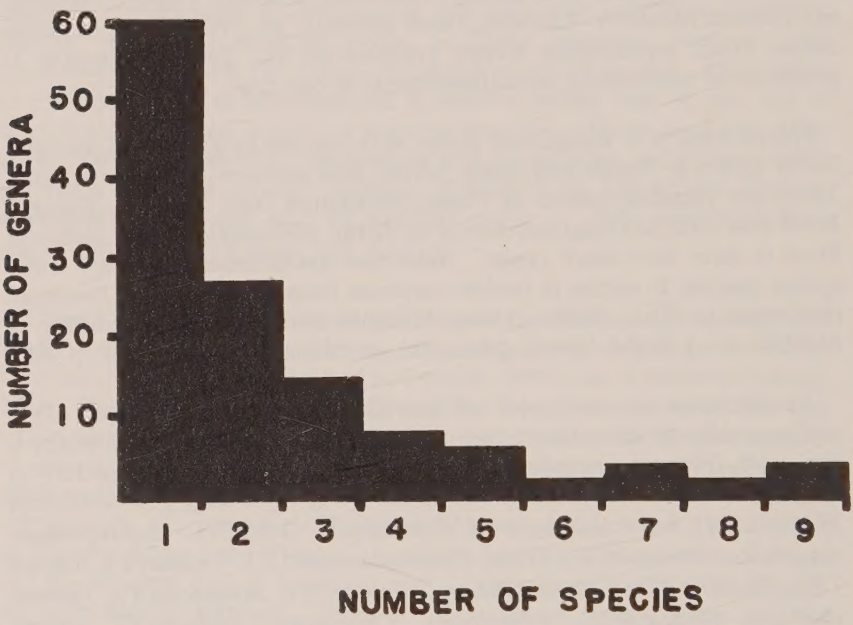

Fig. 2. The size and number of small genera of Compositae in China.

Map 24 illustrates the general pattern of distribution and the areas of concentration of the small genera of Compositae in China. An analysis of the distributional record of these genera reveals that they may be grouped into three types. These are the genera with species in China known only in cultivation, the genera containing only isolated endemics, and the genera with native species in China and also elsewhere in other floristic regions.

Endemics. Thirty-four of the 128 small genera are endemic to China. Their occurrence in various provinces is as follows: Yunnan 15, Szechuan 8, Kansu 6, Sikang and Hopei each 4, Heilungkiang, Kirin, Kweichow, Taiwan and Tibet each 3, Chekiang, Chinghai, Kwangtung, Mongolia, Shansi and Suiyuan each 2, and Hupei, Kiangsi, Ninghsia, Kwangsi and Shensi each 1.

A few of these endemic genera were first described from the Himalayan

Region. Recent collections extend their range to Yunnan, Szechuan, Kweichow, Kwangtung and Taiwan. It is evident that the high mountains bordering Yunnan, Szechuan, Sikang and Kansu (the Meridional Ranges) constitute a center of aggregation for the small genera.

Genera known in China only as cultivated plants. Twenty-one of the 128 small genera of Compositae are known in China only in cultivation. The commonest species belong to the genera *Zinnia*, *Helianthus*, *Coreopsis*, *Cosmos*, *Ageratum*, *Gaillardia* and *Calendula*. In the warmer part of the country, the escaped *Ageratum conyzoides* is naturalized and appears weedy in gardens, fields or along the roadside.

Genera with native species in China as well as in other floristic regions. Seventy-three of the 128 small genera of the Chinese Compositae occur also in central Asia, tropical Asia, Africa, the Pacific Islands, Australia or America. There is no record of their introduction from these regions to China or vice-versa. They were probably dispersed accidentally through man's activities. Five of them have widespread species which are usually considered as weeds. *Eclipta* has only one species in China, and this species has been recorded from thirteen provinces. It is a common weed in cotton or soybean fields and its occurrence in China can be traced back to the ancient historical period. Likewise, *Xanthium*, as represented by *X. strumarium*, occurs in seventeen provinces in China. *Bidens parviflora* occurs in thirteen provinces and *B. biternata* in ten provinces.

However, the majority of these small genera have limited distributions. Map 24 indicates that they concentrate in Taiwan, Kwangtung, Hainan, Chekiang, Hupei, Szechuan, Yunnan, Hopei, Shansi, Sinkiang and, to a lesser extent, in Mongolia, Liaoning and Heilungkiang. A comparison of their distributions outside China and their concentration within the country presents evidence of a correlation between the occurrence of these small genera of Compositae and the courses of the ancient trade routes or the ports of the newer waterways. These correlations are shown by the following statistics:

(1) Within China the distributions of small genera with tropical Asian and African range are like this: Hainan 5, Kwangtung 4, Taiwan 4, Szechuan 3, Yunnan 2, Kweichow 2 and Fukien 1.

(2) Within China the distributions of small genera with pantropical or tropical American range are like this: Taiwan 18, Kwangtung 16, Hainan 14, Szechuan 10, Yunnan 9, Chekiang 3, Fukien 3, Hupei 2, Kiangsu, Kweichow, Hunan and Kwangsi 1 each.

(3) Within China the distributions of small genera with tropical Asian, Pacific Islands and Australian Range are like this: Taiwan 3, Hainan 3, Kwangtung 2, Yunnan, Szechuan and Hupei 1 each.

(4) Within China the distributions of small genera with Central Asian-Mediterranean-European-American Range are like this: Sinkiang 20, Tibet 6, Mongolia 5, Kansu, Shantung, Hopei, Szechuan, and Liaoning each 3, Kiangsu, Kweichow and Heilungkiang each 2, Honan and Anhwei 1 each.

It is interesting to point out that the largest number of the tropical Asiatic or African genera occur chiefly in Hainan, Kwangtung and Taiwan. Their absence from the coastal towns in Chekiang and Kiangsu or the metropolises along the Yangtze River, and their occurrence in Yunnan, Kweichow and Szechuan, indicate that these genera were probably introduced through the ancient trade routes connecting Rangoon (Burma) and Yunnan (MAP 31), or those connecting Hanoi (Indo-China) and Yunnan, thence due north through Kweichow and Szechuan to the ancient Chinese capital, Sian, in Shensi.

The pantropical genera are also concentrated in Taiwan, Kwangtung, Hainan, and, to a lesser degree, in Yunnan and Szechuan. Some of them also occur in Chekiang, Hupei and Kiangsu. It is evident that these genera were introduced to the interior provinces of Yunnan, Szechuan, Kweichow, etc., through the Yangtze waterway as well as through the Burma and Indo-China trade routes.

The most striking facts are centered about the genera with central Asiatic, Mediterranean and European distribution. Of these genera Sinkiang has the largest number, followed by Tibet and Mongolia. Liaoning and Heilungkiang also have some species. It is evident that the distributions of these genera follow the ancient trade routes. The most-used trade routes of ancient China passed through Sinkiang Province, and it is here that the largest number of genera common to China and Central Asia, the Mediterranean Region, and Europe are found.

Tibet is on the main ancient trade route that connected the upper Gangetic Plain, Central Asia and west China. Heilungkiang is on the eastern end of the great Northern Trade Route which connects Manchuria, Siberia, Central Asia and Europe. The occurrence of genera of Compositae which are predominantly central Asiatic, Mediterranean or European indicates that these small genera are adventives to the flora of China.

Regarding the small genera of Compositae in China we may observe that (1) most of the small genera are really small, about 70 per cent of them including only one or two species; (2) slightly over one-fourth of the small genera are endemics, many of them being aggregated in the Meridional Ranges; (3) about half of the small genera are probably adventives introduced to China either through the ancient trade routes or through the more recent waterways.

(*To be concluded*)